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SERIE: FISKERI · BIND XI

Nr. 6. ERIK L. B. SMIDT: ANIMAL PRODUCTION IN THE DANISH WADDENSEA

KØBENHAVN
C. A. REITZELS FORLAG

BIANCO LUNOS BOGTRYKKERI

1951

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SERIE: FISKERI

BIND XI

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Programme of work for the investigations are adopted by "Kommissionen for Danmarks Fiskeri- og Havundersøgelser" (the Danish Committee for Fisheries Investigations and the Study of the Sea) which is appointed by the Minister of Fishery, and the investigations are carried out by the institution "Danmarks Fiskeri- og Havundersøgelser" (the Danish Institute for Fisheries and Marine Research). The Laboratories of "Danmarks Fiskeri- og Havundersøgelser" are situated at Charlottenlund Castle, Charlottenlund.

"Kommissionen for Danmarks Fiskeri- og Havundersøgelser" consists of the following members: Departementschef B. DINESEN, Chairman of the Committee, Permanent Under Secretary of the Ministry of Fisheries.

Dr. phil. Å. VEDEL TÅNING, Vice chairman, Director of "Danmarks Fiskeri- og Havundersøgelser". Fiskeauktionsmester NIELS BJERREGAARD, Chairman of Danish Fishermen's Association ("Dansk Fiskeriforening").

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Fiskeskipper ADOLF JØRGENSEN, Chairman of Skagen Fishermen's Association.

Dr. phil. E. M. POULSEN, Head of Office, "Danmarks Fiskeri- og Havundersøgelser". (Super-numerary (leave of absence) — Executive Secretary of ICNAF).

Fiskeskipper LAUR. THYGESEN, Chairman of Danish Westcoast Fishermen's Association ("Vestjysk Fiskeriforening").

Secretary to the Committee: Kontorchef G. L. MOURIER. Head of Office (Ministry of Fisheries).

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August, 1953.

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MEDDELELSER FRA KOMMISSIONEN
FOR DANMARKS FISKERI- OG HAVUNDERSØGELSER

SERIE: FISKERI · BIND XI · Nr. 6 · 1951

ANIMAL PRODUCTION
IN THE DANISH WADDENSEA

By

Erik L. B. Smidt

KØBENHAVN
C. A. REITZELS FORLAG

1951

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I. Introduction.

In the present paper an attempt is made to give an all-round account of the fauna of the Danish Waddensea, biological aspects of the production having been the guiding principle during the work. The main object was to study the quantity and production of the bottom invertebrates that constitute the food of the abundant stock of young plaice which grow up in this part of the sea during the summer. The chief points to be taken into consideration in this connection are: 1) the reproduction and growth of the bottom fauna, 2) its food supply and feeding habits, and 3) the consumption of the bottom fauna. It is especially points 1) and 3) that are dealt with by the author, while point 2) is treated more summarily on the basis of the available literature.

The Danish Waddensea constitutes the northernmost part of the whole tidal area situated inside the Frisian Islands. Comprehensive biological investigations by Danish and German scientists have shown that these waters must be regarded as the chief nursery ground for the stock of plaice in the North Sea, for which reason fishery-biological studies have been carried on in the Danish Waddensea for a number of years. Since 1936 these investigations have been undertaken by the Marine-Biological Laboratory (Charlottenlund Castle, Copenhagen).

The fundamental ecological studies of the invertebrate fauna of the waddens were made from the Skallingen Laboratory by Dr. H. M. THAMDRUP, and the present paper is a continuation of these investigations, the work in nature having been carried out with the Esbjerg branch of the Skallingen Laboratory as a base. As the work moreover forms part of the fishery-biological investigations carried out by the Marine-Biological Laboratory, it appears as the result of a cooperation between these two laboratories. Furthermore, an essential part of the collected material of bottom animals was worked up by the author at the Natural History Museum of Aarhus.

Acknowledgments.

While this work has been in progress, the author has received help in many ways from various persons.

The directors of the Skallingen Laboratory, Professor NIELS NIELSEN, Ph. D., of the Natural History Museum, H. M. THAMDRUP, Ph. D., and of the Marine-Biological Laboratory, Å. VEDEL TÅNING, Ph. D., besides granting laboratory facilities, have offered me practical, financial, and expert aid in various ways.

Discussions on special subjects with mag. sc. E. BERTELSEN, Professor R. SPÄRCK, Ph. D., and G. THORSON, Ph. D., have been of great value for the present work.

Valuable information on the topography was given me by KAJ HANSEN, Ph. D., and cand. mag. BØRGE JAKOBSEN, and cand. mag. ASGER LUNDBAK has supplied a number of data on the hydrography.

A number of Danish specialists on the various animal groups have helped me to determine the material collected, viz. the late mag. sc. S. A. BOISEN BENNIKE (Oligochaeta), cand. mag. B. DAMSTEDT-CHRISTENSEN (Ostracoda), cand. mag. KAREN BILLE HANSEN (Bryozoa), mag. sc. C. BARKER JØRGENSEN (Lamellibranch larvae), P. L. KRAMP, Ph. D. (Hydroidea), mag. sc. F. JENSENIUS MADSEN (Anthozoa and Echinoderma), mag. sc. ERIK RASMUSSEN (Polychaeta), the late cand. mag. K. STEPHENSEN (Crustacea), mag. sc. ELISE WESENBERG-LUND (Polychaeta), and cand. mag. TORBEN WOLFF (Crustacea). Further, ERIK DAHL, Ph. D. (Sweden) has determined the material of Harpacticoidea.

As regards the printing, H. BLEGVAD, Ph. D., the editor of these publications, has offered me valuable help and guidance.

The translation of the manuscript into English has been done by Miss E. GLEERUP. To all who have thus assisted me I wish here to express my most cordial thanks.

II. Methods and Technique.

While the samples were collected and the observations in nature made with the Skallingen Laboratory at Esbjerg as a base, the further preparation of the material was carried out at the Natural History Museum, Aarhus (from September 1941 to January 1945), and at the Marine-Biological Laboratory, Copenhagen (from January 1943). In the summers of 1942, 1943, 1944, the late summer of 1945, and the summers of 1946 and 1947 the author stayed for long periods at the Waddensea, while at the other seasons of the year his visits there were rather short. The work in nature was rendered extremely difficult during the war years owing to the German blockade of the coastal areas and the whole insecurity caused by the state of war.

The methods of collecting and further treatment of the material of plankton and benthos are described below. The technique of the substratum experiments with larva of *Pygospio elegans* and *Polydora ciliata* is described in chapter VI.

A. Plankton.

1) Collecting and preservation.

At all seasons of the year quantitative collections of plankton were made, as far as possible once a month or even more frequently. The samples were taken with a conical net, which was hauled vertically through the water from the bottom to the surface. The ring of the net was $\frac{1}{5}$ m² in area, and the net itself was made of gauze No. 12, i. e. 12 meshes per mm. Most of the collecting work was carried out from a jolly-boat off the harbour of Esbjerg (depth 7—10 m), but in bad weather the samples were collected from the harbour pier (depth 3—5 m). Samples were taken at low water and at high water in order to ascertain the changes of the plankton with the tide, and on each sampling two or four net-hauls were made.

As soon as the samples had been taken to the laboratory, they were examined under a binocular dissecting microscope, and unknown bottom animal larvae, if any such were present, were drawn under a monocular microscope by means of a drawing apparatus. Afterwards the samples were preserved for a later counting of individuals; for each sampling 1 or 2 hauls were preserved in formalin, and 1 or 2 hauls in alcohol (for the case shell-bearing molluscan larvae should be present).

In addition to these collections, non-quantitative samples were taken on the waddens at high tide by means of a smaller plankton net.

2) Counting.

The counting of individuals was a very time-consuming work because of the great quantities of stirred-up bottom material in the water, especially in the low-tide samples, and no doubt some individuals have been overlooked for this reason. Rather rare species were pipetted up, while more numerous species were counted in a Petri dish with a cross-ruled bottom. Very numerous species were only counted in part of the sample. The content of larvae per m^3 of water was calculated from the height of the water column through which the plankton net was hauled, and the area of the net-ring. If unknown larvae were found, they were drawn.

B. Benthos.

1) Collecting and preservation.

To collect micro bottom samples, a celluloid tube was sunk into the bottom, closed air-tight at the upper end, and pulled out containing a plug of the bottom material. By means of a piston introduced into the tube from below, the material was pressed upwards and out of the tube, and thus a ca. 3 cm long plug of material was obtained as a sample. In a few cases the samples were cut into horizontal sections at intervals of 1 or 2 cm to render possible an examination of the vertical distribution of the microfauna. When the samples were taken on the waddens, the celluloid tube was simply pressed down into the bottom with the hand and closed above with a finger. At this sampling on the waddens, tubes securing 0.95, 2.25, and 5.07 cm^2 of the bottom area were used, of which the samples of 2.25 cm^2 turned out to be the most suitable. When sampling from a boat in the channels (at the fishing stations), the tube was mounted on a 4 m long pole by means of a special apparatus (see fig. 1). The tube was closed above by a rubber valve to prevent the sample from being lost when hauled up. The apparatus was furnished with a horizontal plate with a hole through which the celluloid tube passed, and as soon as this plate touched the bottom, the instrument was hauled up. The celluloid tube was 2.25 cm^2 in transverse section (in the first samplings a tube with a transverse area of 0.95 cm^2 was used). The samples were preserved in formalin and later sorted and counted in the laboratory.

Another apparatus for quantitative collecting of the microfauna was a specially constructed "wadden skimmer" (fig. 2), which secured 25 cm^2 -samples of the upper layer of the wadden. The skimmer consisted of a metal frame, which was placed on the wadden and

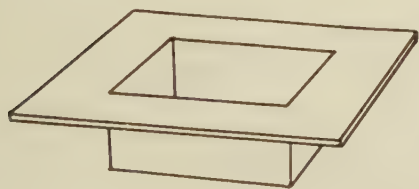


Fig. 2. "Wadden skimmer" (cf. the text).



Fig. 1.
Micro
bottom
sampler
(cf. the
text).

fixed by means of a vertical edge (issuing from the inner side of the frame), which was pressed down into the bottom. The frame enclosed 25 cm^2 of the bottom, from which the uppermost layer was "skim-

med off" by means of a trowel. This skimming apparatus was used for quantitative sampling of *Hydrobia ulvae* and the youngest bottom stages, whose habitat is precisely the uppermost bottom layer, but only in a few cases was it used for sampling of the real microfauna. The number of skimmer samples per station was generally four. For preservation, alcohol or neutralised formalin was used.

For a non-quantitative collecting of the microfauna on the waddens (especially for the purpose of securing the youngest bottom stages of *Arenicola*) I walked on the bottom at high tide, drawing a plankton net after me, while at the same time I whirled up the bottom material into the water.

Various implements were used for the quantitative collecting of the macrofauna. The instrument most frequently employed on the waddens was a core sampler securing $\frac{1}{100}$ m² of the bottom (a metal cylinder which was thrust 10–15 cm down into the bottom and then dug out with a small spade). These samples were washed in a sieve with a mesh-width of 1 mm, after which the rest (animals and coarser bottom material) was transferred to glass vessels and preserved. In some cases a sampler taking $\frac{1}{20}$ m² was used, and the sample was then washed in a coarser sieve (mesh-width 6 or 1.9 mm). The amount of *Arenicola* was determined by counting the heaps of excrements over several small areas ($\frac{1}{5}$ m²) at each station. These methods for the estimation of the macrofauna are the same as were used by THAMDRUP (1935).

In the channels, samples of the macrofauna were taken by means of the van Veen bottom sampler, which, as shown by THAMDRUP (1938), secures three times as large quantities by weight of the bottom fauna as the Petersen grab, because it penetrates to greater depths. The samples were washed in sieves of different mesh-widths (smallest width 1.9 mm). In some cases $\frac{1}{10}$ of the sample was washed in the same fine-meshed sieve as was used for the $\frac{1}{100}$ cm² samples from the waddens. These $\frac{1}{10}$ samples were taken from a specially constructed "de-

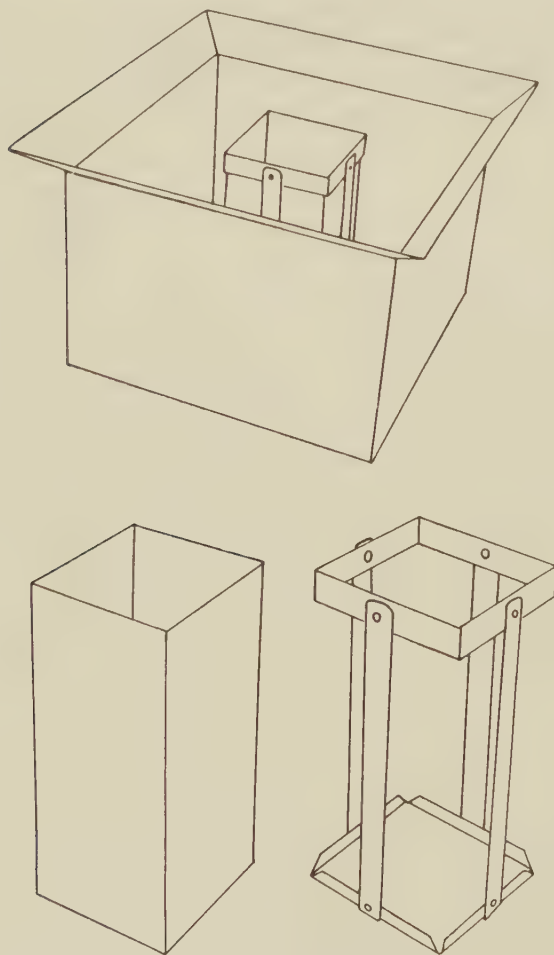


Fig. 3. Above: "Decimal box" (bottom 30 × 30 cm) with a $\frac{1}{10}$ sampler placed in it. — Below: The $\frac{1}{10}$ sampler and its stand.

cimal box" (fig. 3), a metal box with a quadratic bottom, into which the contents of the bottom sample is poured. The smaller samples were taken by means of a quadratic sampler securing $\frac{1}{10}$ of the contents of the box. In order to close the sampler at the bottom, a metal stand, furnished with a plate with low vertical edges, is placed in the box before the sampler is lowered into it.

The samples of the macrofauna were generally preserved in formalin, but in some cases shell-bearing molluscs were preserved in alcohol.

In addition to the quantitative samples, some samples were taken with a dredge in the channels for faunistic investigations.

2) Sorting and counting of individuals.

On sampling the microfauna, the animals and the bottom material were preserved together. The subsequent sorting in the laboratory was done by stirring up the material in a glass dish with water and then letting it settle; the organisms would then form the upper layer, which could be poured off into a Petri dish after most of the water had been pipetted away. This method was repeated until no animals were left in the bottom material. The counting of the individuals was done in the same way as the counting of the plankton animals. From each sample a representative collection of animals was pipetted up. In samples containing large quantities of fine particles, these latter would settle more slowly than the animals, so they could be pipetted off together with the water.

The samples of the macrofauna were transferred to flat enamel trays and were sorted by means of a pair of tweezers.

3) Weighing.

The weighing of the microfauna was carried out at the Zoophysiological Laboratory of the University of Copenhagen. The *Harpacticoida* and *Ostracoda* were weighed in great numbers in representative collections, from which the mean weights per specimen were calculated, and these weights were then used in determining the quantity per m² of the bottom at the different stations. 2000 *Harpacticoida* freed from water on a piece of filter paper weighed 19.8 mg, which gives a mean weight of 0.0099 mg. A number of 185 *Ostracoda* treated in the same way had a mean weight of 0.012 mg. The weight of the *Nematodes* was found by determining the volume, the specific weight being taken to be 1. The method used is that devised by C. OVERGAARD NIELSEN (1949, pp. 14—15). The lengths of some specimens of different size were measured by drawing the animals with a drawing apparatus under a monocular microscope. As the animals are circular in transverse section, the volume can be found by multiplying the length with the mean transverse area. OVERGAARD NIELSEN (l. c.) found that the diameter at the middle of the oesophagus corresponded to the mean diameter, and this measurement was then used for the determination of the volume. The mean weight of the small *Nematodes* was found to be 0.6 gamma, that of the bigger *Nematodes* 7.8 gamma. As big *Nematodes* are present in the samples in larger numbers than the small ones, the mean weight of the *Nematodes* was fixed at 5 gamma, which figure was used in determining the quantities by weight per unit area of the bottom.

On weighing the macrofaunal animals, these were first dried with filter paper. As for *Arenicola*, the weights were found by multiplying the numbers of individuals by 4, as 4—4.5 g corresponds to the mean weight of the animals investigated by THAMDRUP (1935) at Skallingen.

4) Measurements of growth.

In several species the individuals from representative samples collected at different times of the year were measured in order to obtain information of the growth. The *Polychaeta* were measured in their full length in the preserved condition (*Arenicola* preserved in alcohol, the others in formalin). In *Hydrobia* and *Littorina* the height of the shell, and in *Cardium* the length of the shell were measured.

III. Topography and Hydrography.

A. Topography.

The Danish Waddensea¹⁾, situated along the southern part of the west coast of Jutland, with its 835 km² constitutes the northernmost part of the North European Waddensea, which extends from the mouth of Varde Aa in the north to den Helder on the Dutch North Sea coast. Here, in the lee of the chain of Frisian Islands, there are extensive tidal flats, called waddens, which in the Danish part constitute about 60 per cent. of the area.

The Danish Waddensea is bounded on the east by the mainland. Its western boundary extends from the peninsula of Skallingen along the west coasts of the North Frisian Islands, while its southern boundary is formed by the Danish-German frontier. Its northernmost portion is Ho Bay (= Ho Bugt on the map in fig. 41, p. 122), situated north of Graadyb and inside the peninsula of Skallingen; here the outflow of fresh water (from Varde Aa) is felt more than in the remaining part of the area.

In 1939 the building of a dam between the mainland and Rømø was started; it was completed in 1946. The dam is indicated on the map in fig. 4, but as it was not completed when the investigations were carried out in the southern Danish Waddensea, the conditions in 1941 are shown on the map.

The waddens (or wads), defined as the areas that become dry at low water, may, on the basis of the condition of the bottom, be divided into 1) those with a firm sandy bottom, 2) those with a soft muddy bottom, and 3) those with a mixed bottom (see the map in fig. 4). This grouping is as far as possible in agreement with that made by GRY (1942, p. 20). The map only shows the distribution of the wadden types in broad outline, as more detailed investigations of them are lacking. The map has been drawn on the basis of the paper by GRY (l. c.), TRAP: DANMARK (1927, Hft. 4, p. 217), and verbal information furnished by collaborators at the Skalling Laboratory, notable Mr. KAJ HANSEN and Mr. BØRGE JAKOBSEN. It appears from the map that the greater part of the area of the waddens has a firm sandy bottom or a mixed bottom, while a soft bottom is only found in particularly sheltered places.

As regards the character of the sediments in the Danish Waddensea, KAJ HANSEN (1951) states that even where the bottom is soft, the normal sediment on the wadden is sand. Deposition of slik (mud) may take place, on a larger or smaller scale, under very special conditions, for instance in the old silting-up channels along the eastern side of the islands and in Ho Bay, where old salt marshes are eroded. The very limited areas with pure slik waddens situated here are not real slik waddens, but more probably old salt marshes the upper layer of which has been removed by erosion, so that the surface now lies at such a low level that it will only dry up at low tide.

Patchy growths of *Zostera marina* occur in several places on the waddens, and in these patches the bottom is most often of a mixed character. This is, for instance, the case on the inner part of the sand wadden north of Fanø, where a great many of the investigations were carried out.

The channels are the areas that are permanently flooded, and they present greatly varying depths. The greatest depths in the four large deeps, Graadyb, Knude Dyb, Juvre Dyb, and Lister Dyb, are 17, 15, 17, and 35 m, respectively, but just outside these deep areas, in the North Sea, there occur sand barriers with threshold depths at low-water springs of 6.5, 3, 3, and 7 m, respectively. If we go from the deep areas into the Waddensea, the depth de-

¹⁾ Danish: Vadehav; Dutch: Waddenzee; German: Wattenmeer.

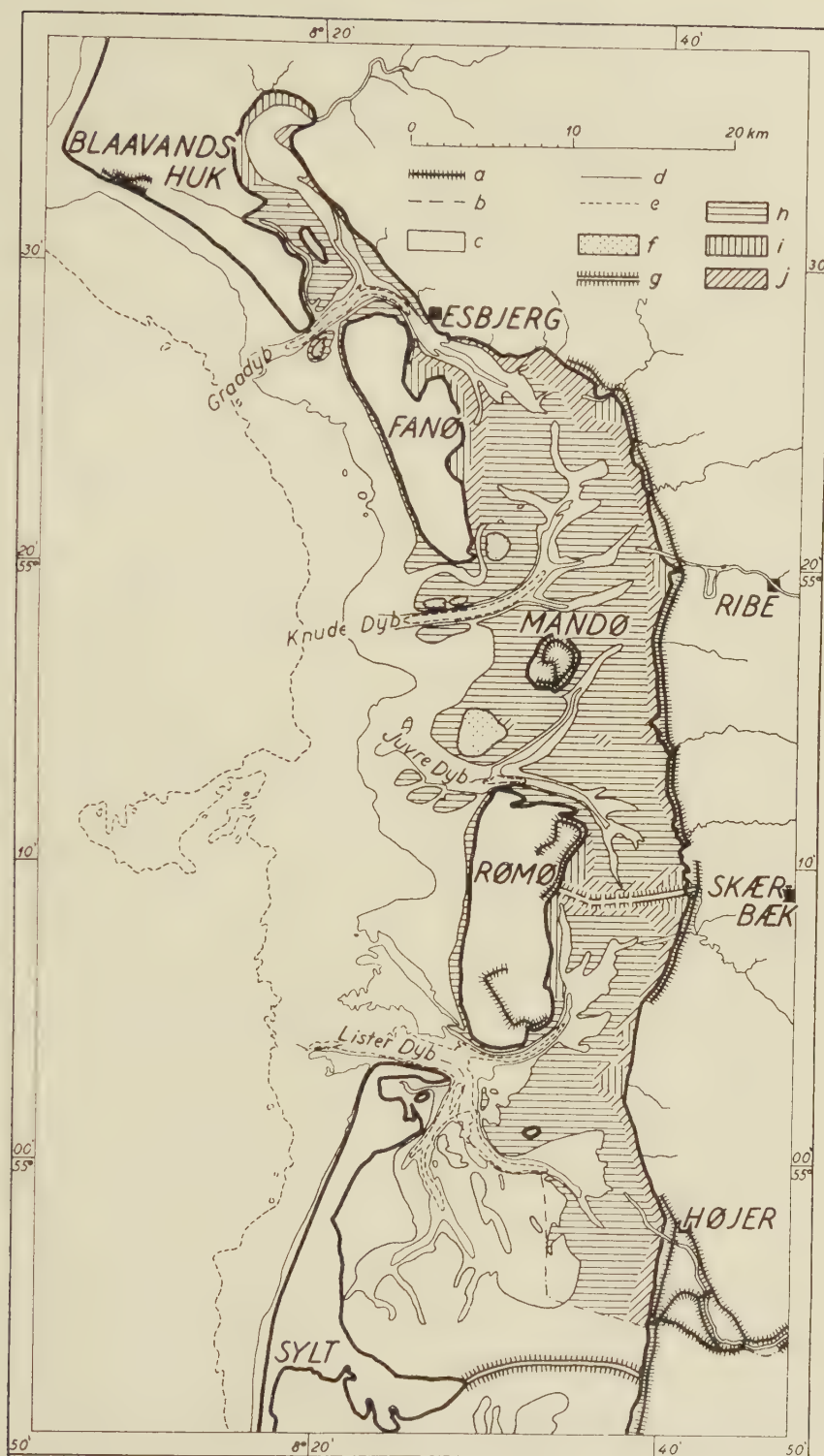


Fig. 4. Outline map of the Danish Waddensea showing the different types of wadden. The map represents the conditions in 1941 when the large collections were made, the part of the Rømø dam indicated by a broken line being built later. (a = dike, b = Danish-German frontier, d = 4 m depth contour, e = 10 m depth contour, f = high sands, i.e. sand areas not flooded by the daily high-tide, g = dam, h = sand waddens, i = soft waddens, j = mixed waddens.)

creases rapidly, and in by far the majority of channels the depth is less than 6 m, reckoned from the mean low-water spring.

The character of the bottom in the channels is little known. In most places it consists of more or less coarse sand (GRV l. c., p. 21, fig. 6 F), but in some places (e. g. in Ho Bay) it may be very fine-grained and clayey.

B. Hydrography.

The information about the hydrography given here was in the main supplied by Mr. A. LUNDBAK (Meteorological Institute, Copenhagen), whose studies have not yet been published. This information has been supplemented by data from the available literature, particulars supplied by Dr. H. M. THAMDRUP, and some few of the author's own observations.

1) The tide is the dominant hydrographic factor. According to information supplied by Mr. LUNDBAK, the height of the tide (i. e. the difference between the lowest and the highest water-level) in the Danish Waddensea is ca. 165 cm. It is somewhat greater in the southern than in the northern part. Thus a self-recording water-gauge, placed in Højer Dyb during two summer months of 1941, showed an average height of the tide of ca. 175 cm, while the self-recording water-gauge at Esbjerg in 1940—41 showed a mean height of 150 cm.

2) The currents are chiefly tidal currents. The rising tide flows in through the four large deeps (Graadyb, Knude Dyb, Juvre Dyb, and Lister Dyb) and onwards through the channels, whence it flows across the waddens. The falling tide moves out the same way.

In addition to the tidal currents there is a north-moving residual current in the Waddensea parallel with a likewise north-going current outside the chain of islands.

By means of current measurements in connection with the variation of the salinity during a tidal period (see below) we may get an idea of the movements of the water masses. The velocity of the tidal currents is very considerable, and when greatest, they flow at a rate of 2—3 miles an hour through the aforementioned four deeps. This means that a considerable water exchange takes place with the North Sea, which as to the area of Graadyb may be illustrated by some current-maps prepared by LUNDBAK (fig. 5 A + B). The maps show influx and efflux, respectively, one hour before and one hour after the highest water level. These two points of time were chosen because precisely at these times the force of the current corresponds fairly well to the mean value of the particular tidal phase, and because the water level is then so high that we may obtain a picture of the water movement over the waddens.

Thus we may assume that a water mass which at high-water occurs off the harbour of Esbjerg, will, at the succeeding low-water, be found entirely outside Graadyb.—It is evident that this considerable exchange of water between the Waddensea and the North Sea is of great importance for the transport of planktonic organisms, including pelagic bottom animal larvae (see chapter VIII).

3) The salinity is generally a little lower in the Waddensea than in the adjoining part of the North Sea, and it decreases somewhat from the deeps shorewards owing to affluents from the rivers; it is, however, only in the innermost part of Ho Bay, where Varde Aa debouches, that quite low salinity values are found. Moreover there is an appreciable variation in the salinity with the movements of the tide.

LUNDBAK states that the mean salinity of the western boundary line of the Waddensea in summer is scarcely 31 per mille, in winter somewhat lower. In the nearby part of the North Sea (Vyl lightship) the salinity mostly ranges between 32 and 33 per mille.



Fig. 5 A. The flood tide one hour before the highest water level. (After LUNDBAK, unpublished work).

According to information from H. M. THAMDRUP about investigations carried out from March 1935 to February 1937 (both months inclusive), the following average salinities were found (average of measurements both at low-water and at high-water) at Esbjerg and at Ho (northern part of Ho Bay):

	Summer (June-October)	Winter (November-May)
Esbjerg (March 1936—February 1937)	28 per mille	25 per mille
Ho (January 1935—February 1937)	25 — —	18 — —

These figures show the decreasing salinity towards the interior of Ho Bay, and in addition they show that the mean salinity is greater in the summer half-year than in the winter half-year. An entirely corresponding annual variation is shown by investigations made at Sylt (MÖBIUS 1893, p. 70). This variation in the salinity is due to the larger outflow of river water in the winter half-year and the more intense evaporation in the summer half-year.

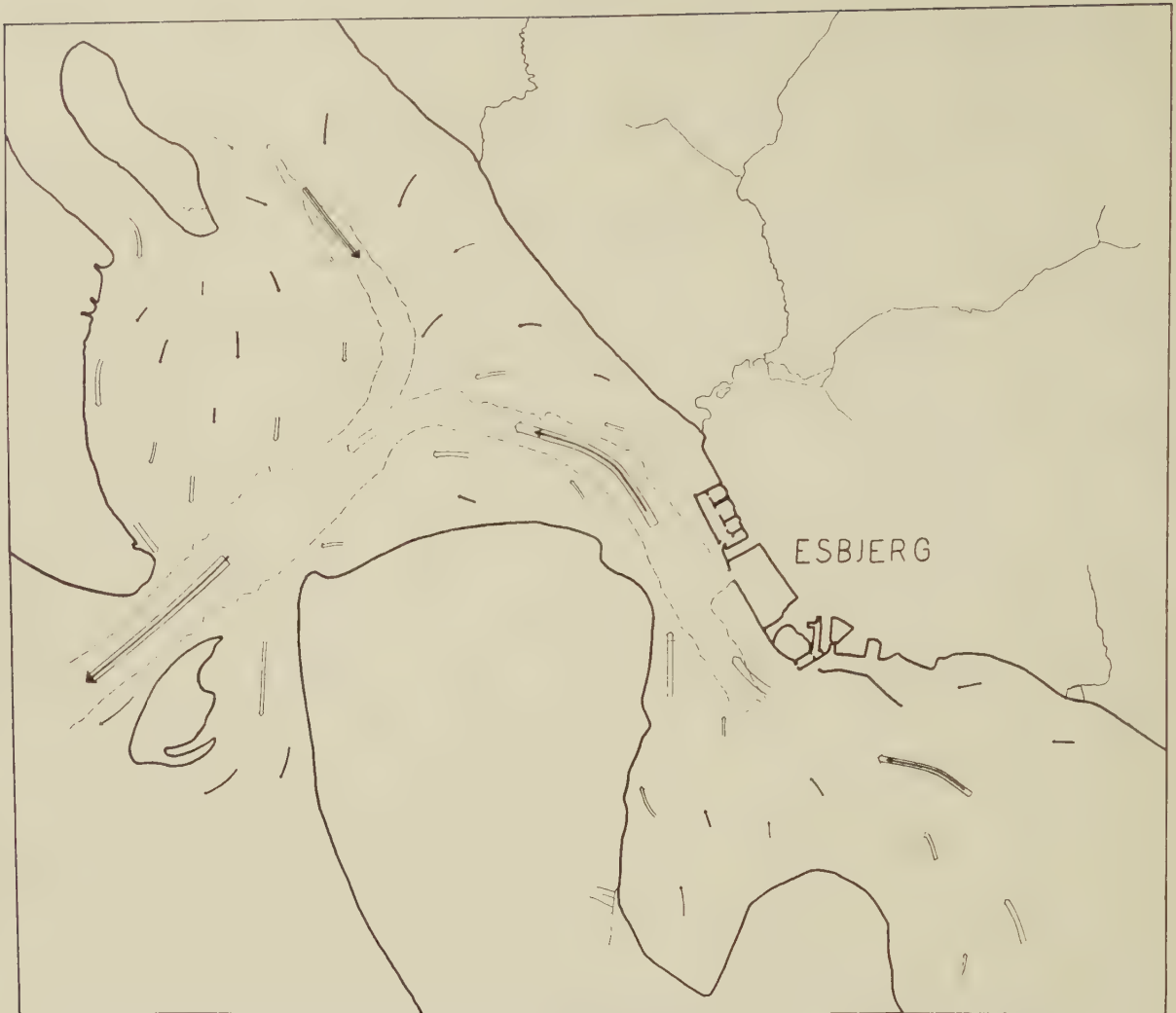


Fig. 5 B. The ebb tide one hour after the highest water level. (After LUNDBAK, unpublished work).

For various reasons the salinity undergoes considerable variations. The most conspicuous are the tidal variations, which, however, are only fairly great in the interior of Ho Bay. This is best illustrated by some maps prepared by LUNDBAK (fig. 6), showing that the salinity in the innermost part of Ho Bay at low-water may even fall to less than 10 per mille, while at high-water it may rise to more than 20 per mille. The maps further provide a distinct picture of the movements of the water masses within a tidal period (cf. above under Currents).

The salinity conditions described above principally have reference to the channels. If we look at the conditions on the waddens, the picture will be complicated by variations of a more casual character, since certain factors may give rise to especially high or especially low salinities. Especially high salinities occur when dry winds blow across a wadden with a quite thin covering of water, or when intense sun radiation for some time affects isolated pools. On a wadden off Brøns, LUNDBAK in July 1942 measured a salinity of 37.35 per mille in a sample taken at a depth of 1—2 cm; and as an extreme case LUNDBAK states that on an inner

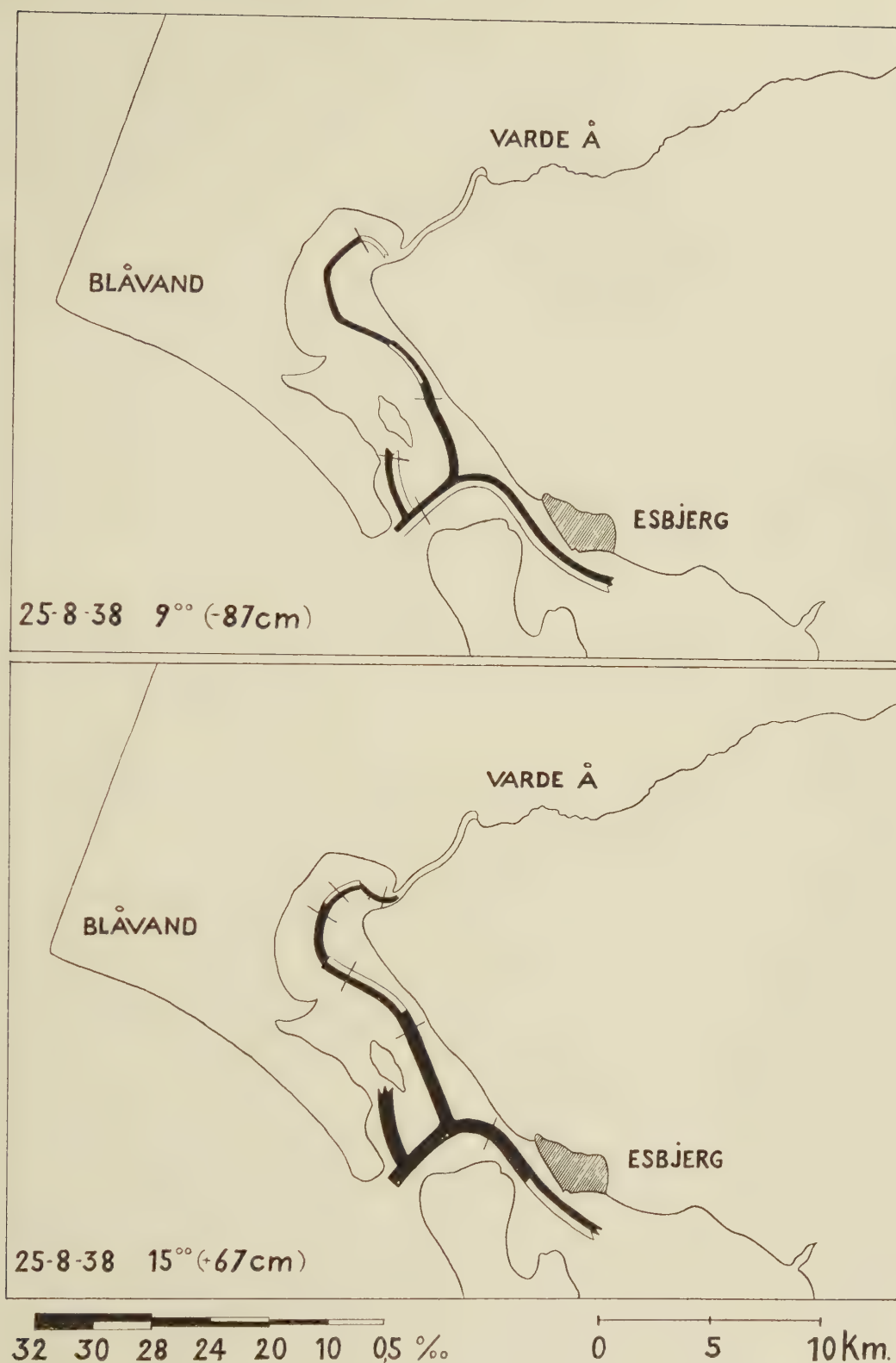


Fig. 6. Distribution of salinity at the bottom of the Graadyb area and in Ho Bay at lowest (map above) and highest (map below) water level for the same tidal period. (water level -87 cm at 9 o'clock and $+67$ cm at 15 o'clock). The corresponding surface salinities, which are, as a rule, a little lower, are indicated by transverse lines. (After unpublished work by LUNDBAK).

wadden at Skallingen, in a pool which had been isolated for a rather long period of low water level, a salinity of no less than 200 per mille was measured. EBBA THAMDRUP (1935, p. 196) gives some figures from Skallingen for the increase of the salinity resulting from the evaporation during one tidal period. Conversely, the waddens may be covered by a practically fresh water layer when a heavy shower falls on a dry wadden; however, this fresh water layer, according to EBBA THAMDRUP (l. c.), does not seem to cause any change in the salinity of the ground water of the wadden apart from the very uppermost layer. Nor would it seem, according to EBBA THAMDRUP (l. c.), that any admixture of fresh water from the nearby land can be traced in the ground water of the wadden.

4) The temperature of the Waddensea shows much greater variations than that of the open sea outside. Moreover, summer maxima and winter minima set in earlier in the Waddensea than in the sea outside it. Fig. 7 (after H. M. THAMDRUP) shows the difference between the annual variation of the surface temperature at Esbjerg and in the North Sea outside. On the waddens the temperature variations are even much greater than in the channels, since over the waddens they follow the weather conditions for the time being to a much greater extent. According to THAMDRUP (1935) the temperature of the uppermost, moist, layer of the wadden

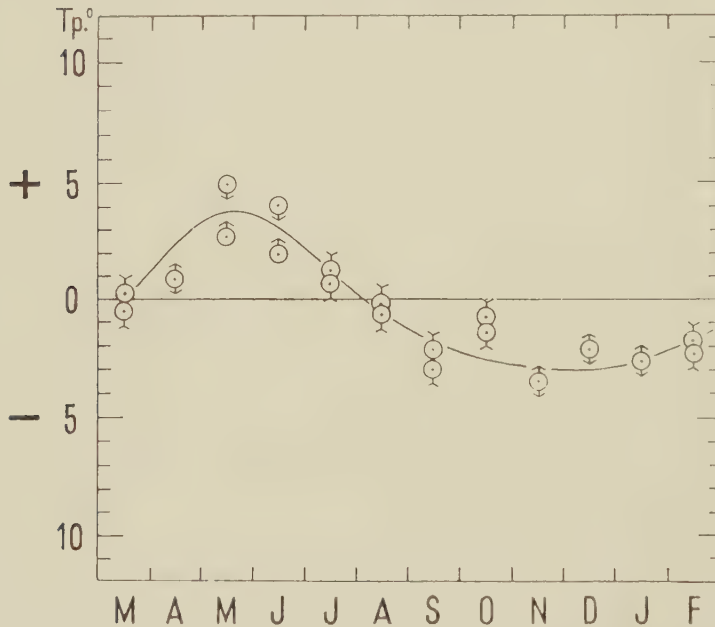


Fig. 7. The difference between the surface temperature at Esbjerg and the Vyl lightship outside Graadyb (horizontal line) during the year. (Prepared by H. M. THAMDRUP and published by SMIDT 1944 B).

ranges between the temperature of the water in the channel and the air temperature, being even nearest the latter; thus the annual temperature variations on the wadden areas are much greater than in other marine biotopes.

In summer the waddens may become very much heated. But already early in the year high temperatures may make themselves felt and thus have a stimulating influence on animal life. Some temperature measurements may serve to illustrate this: On a clear, sunny day (April 4th, 1948) the wadden north of Fanø during the low-water period was covered by a thin water layer of ca. 2 cm. At the middle of the low-water period (13–14 h.) water temperatures ranging between 19.6° and 20° C. were registered, while the water temperature at the edge of the wadden on the boundary to

the open sea was 14.7° C., and at Esbjerg harbour the surface temperature on the same day, at ca. 16.5 h., was only 9.6° C. On the same wadden the following temperatures were measured in the afternoon of June 13th, 1948, likewise at low-water: 28.9°, 31.8°, and 28.9° C., while at the edge of the wadden a temperature of 29.2° C. and at Esbjerg harbour pier 20.1° C. prevailed. These figures show distinctly the heating effect of the radiation of the sun on the wadden areas, and that it makes itself felt already early in the year. As will be shown in chapter VIII,

(p. 108) the effect of this heating early in the year will be that a great many species of the wadden fauna are stimulated to spawn in the months of spring.

Long periods of severe frost will cause the surface of the wadden to freeze down to a depth of several decimetres, which may have catastrophic consequences to the animal stock (SMIDT 1944 B). On February 2nd, 1947, a wadden north of Esbjerg was found to be frozen down to a depth of 18–20 cm, and in the succeeding long period of frost it must have become frozen down to much greater depths. A worm-digger on Fanø reported that the wadden there had been frozen to a depth of ca. $\frac{1}{2}$ m that winter. During the time that investigations of the bottom fauna of the waddens have been carried on, the effects of the following severe winters have been traced: 1928–29, 1939–40, 1940–

41, 1941–42, and 1946–47. To give an idea of the severity of these winters the amount of cold for the winters 1927–28 to 1949–50 for Nordby on Fanø is recorded in table 1 (after “Is- og Besejlingsforholdene i de Danske Farvande” (annual publications)).

Table 1. The amount of cold (i. e. the product of the mean temperature in the frost period and the number of days in the same period) at Nordby (Fanø).

Winter	Amount of cold	Winter	Amount of cold
1927/28	128.3	1939/40	349.9
1928/29	325.2	1940/41	297.2
1929/30	23.9	1941/42	456.7
1930/31	72.8	1942/43	50.7
1931/32	63.5	1943/44	?
1932/33	94.2	1944/45	30.5
1933/34	34.2	1945/46	99.7
1934/35	37.7	1946/47	377.2
1935/36	50.3	1947/48	55.8
1936/37	79.4	1948/49	21.1
1937/38	35.9	1949/50	54.5
1938/39	61.6		

IV. The Fishery-biological Importance of the Waddensea.

A. The economic importance of the Waddensea.

In several ways the Waddensea is of economic importance. A great many species of fish (*Pleuronectes platessa*, *Limanda limanda*, *Anguilla anguilla*, *Belone belone*, and *Scomber scombrus*) are fished on a small scale, and a special trade is digging for lugworms (*Arenicola marina*), which are valuable as bait. The worms are dug out of the wadden at ebb-tide, to be bought, subsequently, by exporters, who forward them to other parts of the country. In quite recent times (since October 1949) a special fishing of *Asterias rubens* has been started in Ho Bay off Hjerting, but ceased in the summer of 1950, the greater part of the stock having been fished up. The catches were sold to the herring oil factory and the meat fodder factory at Esbjerg (cf. further chapter VII).

The Waddensea has its greatest economic importance, however, as a nursery ground for young flatfish, which in the summer half-year come in to the shallow water to feed. Among these, *Pleuronectes platessa* is both the most numerous and the most valuable economically; but *Limanda limanda*, also, is present in considerable numbers, while *Pleuronectes flesus* is less abundant. In addition to flatfish, considerable quantities of young *Clupea harengus* and *C. sprattus* are met with in summer.

B. General characterisation of the fish fauna.

Of the young fish which in summer come into the Waddensea, *Gadus callarias* may be mentioned in addition to those enumerated above. As summer visitors may further occur a

number of the two shoal-fish, *Belone belone* and *Scomber scombrus*, both of which are still caught together with *Pleuronectes platessa* and *Limanda limanda* in so-called "skullergaarde" in the southern part of the Danish Waddensea¹).

Of fish species more stationary, but of no, or only little, economic importance, mention should be made of *Agonus cataphractus*, *Ammodytes tobianus*, and *lanceolatus*, *Centronotus gunellus*, *Cottus scorpius*, *Gobius minutus* (present in enormous quantities), *Syngnathus rostellatus*, and *Zoarces viviparus*.

To complete the picture, a list will be given here of the species, observed in the investigations carried out by the Marine-Biological Laboratory; the designations of frequency are based on the frequency of the fish in catches made with the young-plaice trawl mentioned below (ccc = especially numerous, cc = numerous, c = common, + = few in numbers, r = rare): *Anguilla anguilla* L. (c), *Agonus cataphractus* L. (c), *Ammodytes tobianus* L. (c), *A. lanceolatus* LESAUVAGE (+), *Belone belone* LINNÉ LONNBERG (r in the catches, as it avoids the trawl), *Caranx trachurus* L. (r), *Conger vulgaris* CUVIER (r), *Cottus scorpius* L. (c), *Centronotus gunellus* L. (c), *Clupea harengus* L. (cc), *Clupea sprattus* L. (+?), *Cyclopterus lumpus* L. (r), *Entelurus æquoreus* L. (+), *Gasterosteus aculeatus* L. (c), *Gadus callarias* L. juv. (c), *G. merlangus* L. (c), *G. aeglefinus* L. (r), *Limanda limanda* L. (cc), *Liparis* sp. (r), *Mikrostomus kitt* WALBAUGH LONNBERG (r), *Onos cimbrius* L. (+), *O. mustela* L. (r), *Osmerus eperlanus* L. (c), *Pleuronectes platessa* L. (ccc), *P. flesus* L. (c), *Petromyzon* sp. (+), *Raja* sp. (+), *Rhombus maximus* L. (r), *Scomber scombrus* L. (not taken in the young-plaice trawl, as it avoids this trawl), *Scophthalmus rhombus* L. (—), *Solea solea* LINNÉ LONNBERG (+), *Spinachia spinachia* LINNÉ SAUVAGE (+), *Syngnathus rostellatus* NIELSSON (c), *Trigla gurnardus* L. juv. (r), *Zeugopterus norvegicus* GÜNTHER (+), *Zoarces viviparus* L. (c).

This list of species can be supplemented by the following species (after JOHANSEN 1922 B): *Galeus vulgaris* Fleming, *Liparis liparis* L. and *montagui* Donovan, *Salmo salar* L., *Squalus acanthias* L., *Syngnathus typhle* L., and *Trachinus draco* L.

C. The growth conditions of young plaice in the Waddensea.

The account below is mainly an abstract of the available literature (BRUUN 1927, BÜCKMANN 1934, GARSTANG 1909, HEINCKE 1913, JOHANSEN 1908, 1912, 1913, and 1922 A and B, LÜBERT 1925, THAMDRUP 1936, TÅNING 1943, 1945, and 1947). In addition, unpublished data from the records of the Marine-Biological Laboratory have, with the permission of Dr. TÅNING, been drawn on to a considerable extent.

The life-history of the North Sea plaice is briefly as follows: The eggs are spawned in various spawning areas, mainly in the months of February—March; the most important areas are found in the southern part of the North Sea towards the Channel. From these spawning areas the fry migrates to the Dutch, German, and Danish coasts, in part drifting with the current. During the summer the quite young plaice seek their food in the shallow water. In the autumn they migrate to deeper water, to return next summer—though in smaller numbers—to the shallow water. Gradually as the plaice grow older, they go out towards deeper water; but three-year-old plaice may still frequently be seen in the Waddensea. The migration away from the land with increasing age has been illustrated in an instructive way by GARSTANG (1909) in a map of the distribution of plaice according to size groups and age groups (see

¹) This kind of fishing, which is now prohibited in the remaining part of the Waddensea, takes place by means of V-shaped hurdles placed on the waddens with the mouths pointing shorewards, so that, when the water recedes, the fish found inside them will be caught.

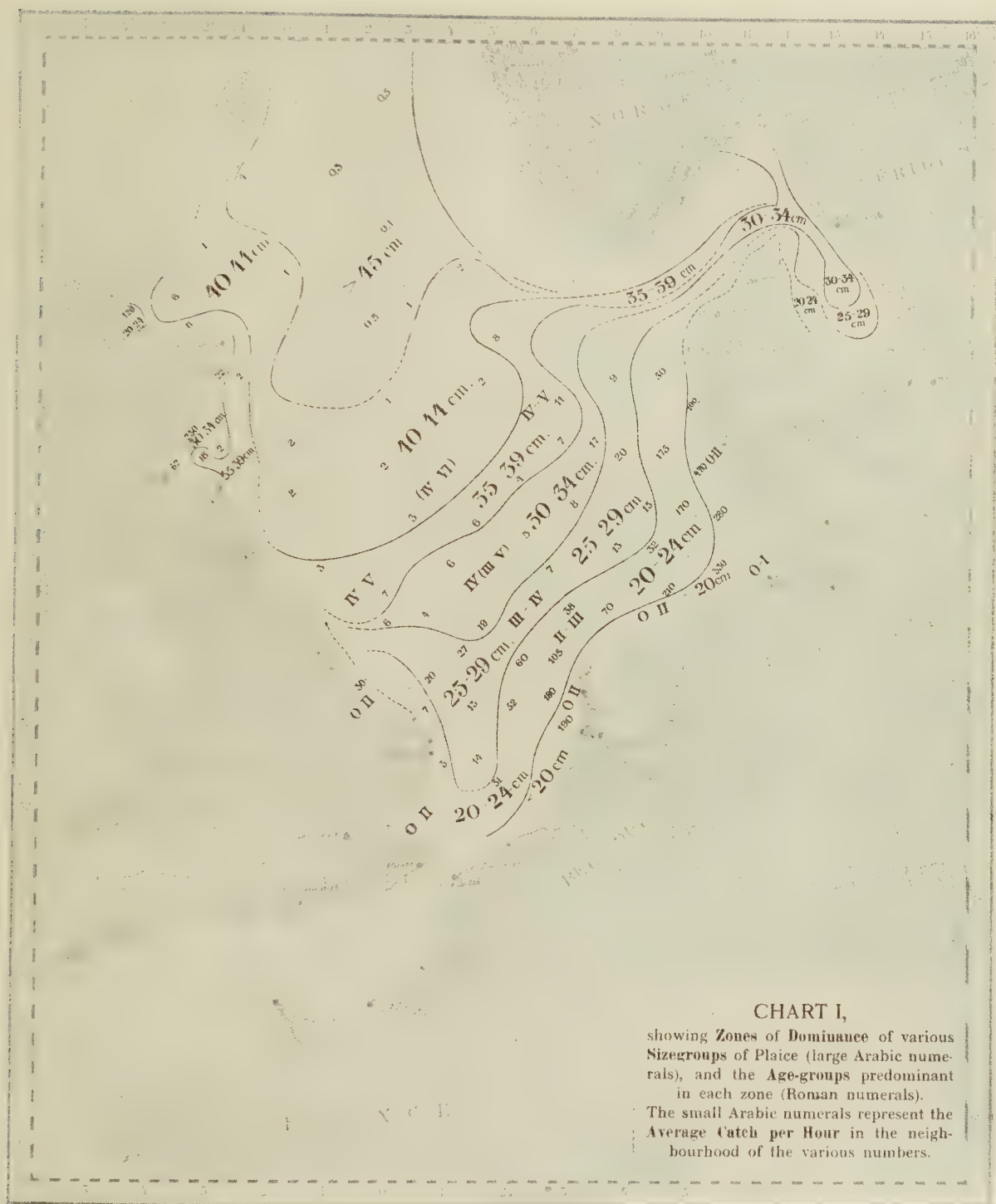


Fig. 8. After GARSTANG 1909.

fig. 8). GARSTANG's map was prepared on the basis of a very copious material (2408 trawl hauls) collected in the years 1902–07 by Belgium, Denmark, England, Germany, Holland, Scotland, and Sweden. It is stated that the map agrees more closely with the conditions in the summer half-year than in the winter half-year.

Only along the coast stretches where food is abundant are large quantities of young plaice to be met with. JOHANSEN (1908) states that 0-group plaice are found along the whole

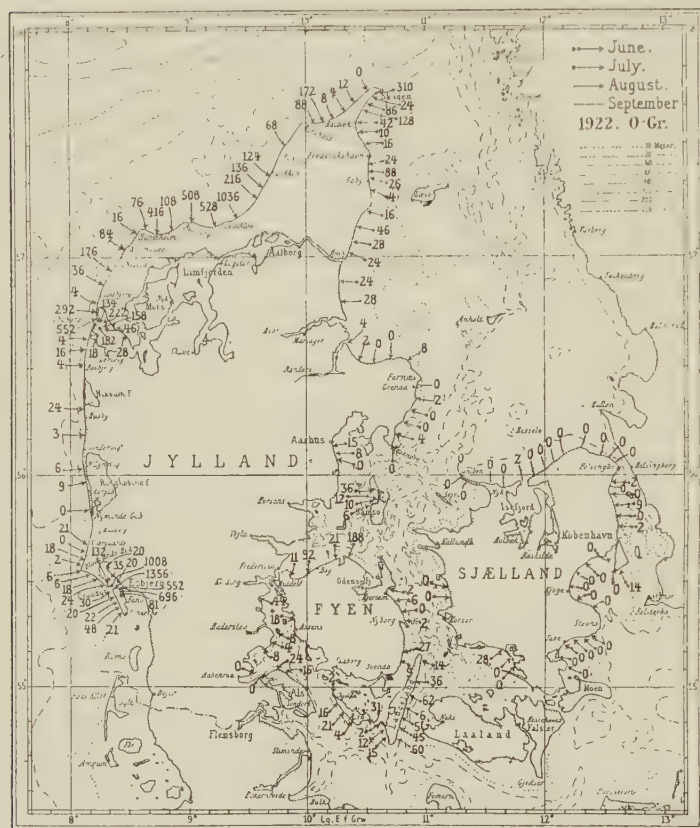


Fig. 9. Distribution of 0-group plaice along the Danish coasts 1922. Figures denote numbers caught per hour with the young plaice trawl. (After BRUUN 1927).

west coast of Jutland at depths between 0 and 5 m, but that they are most numerous in the coastal waters at Thyboron and Esbjerg. The map in fig. 9 (after BRUUN 1927) gives a good idea of the quantity of 0-group plaice in the Waddensea as compared with other coast stretches. It appears from the map that besides in the Waddensea, considerable quantities are found at Thyboron and in the Jammer Bay. These fishery experiments—like those later made by the Marine-Biological Laboratory—were made with Johansen's young-plaice trawl (JOHANSEN 1922 A, BLEGVAD 1936).

From the German Waddensea LÜBERT (1925) and BÜCKMANN (1934) have described the immigration and growth of young plaice, and shown that here, too, they are present in very large quantities in the summer half-year. Thus BÜCKMANN (l. c.) has taken as many as 6000 0-group plaice in an hour's haul with the young-plaice trawl.

As pointed out by JOHANSEN (1913) the immigration of the young plaice in summer into the shallow

water is a migration in search of food. And it is, in fact, only at this season of the year that the growth takes place, growth investigations showing an arrest of growth during the months October–May (BÜCKMANN 1934). The same is shown by unpublished investigations carried out by the Marine-Biological Laboratory.

Generally the immigration of 0-group plaice begins in June and continues during the whole summer. Investigations in the Danish Waddensea have shown that the 0-group plaice are, as a rule, present most numerous in the months of August–October, after which time the number decreases (TÅNING 1943 and 1947).

The distribution of the immigrated plaice in the Waddensea will be of importance for an understanding of their biology. BÜCKMANN (1934) has shown that at rising tide the young

plaice leave the channels and spread over the waddens. At low-water they are found at small depths outside the edge of the waddens, only extremely few 0—II-group plaice being met with at a depth of 7 m or more in summer. In the months of November, December, and March, however, large quantities of these small plaice have been caught at depths greater than 7 m, which shows that in the winter half-year the plaice migrate from the shallow water to greater depths.

This picture of the distribution of the plaice in the Waddensea is confirmed by the investigations carried out by the Marine-Biological Laboratory; I have therefore, to elucidate the question, extracted some observations from the journals of the Laboratory:

The occurrence of the plaice over the waddens has been shown by fishing over the wadden areas. Thus on September 18th, 1938, a trawl was hauled across a sand wadden (Langli Sand), where 21 specimens of plaice (18 0-group individuals and 3 older ones) were caught. In the same locality 37 plaice (16 of the 0-group and 21 older individuals) were taken by trawl on September 22, 1943. In addition to these experiments with trawl, a series of experiments were carried out with V-shaped fixed nets, which were placed on the wadden (Langli Sand) with the mouths turned shorewards, on the same principle as the above-mentioned "skullergaarde", the nets catching the fish occurring over the wadden when the water is falling. In these experiments both plaice and dab (*Limanda limanda*) and a number of other species of fish have been caught. Unfortunately the nets have not functioned so satisfactorily that it is possible, on the basis of the experiments, to say anything about the number of fish that are found over a wadden-area during the high-water period.

Like the investigations of BÜCKMANN (l. c.), the investigations of the Marine-Biological Laboratory have shown that at low-water the young plaice crowd together at comparatively small depths outside the waddens, while they are present in small numbers, only, in the deeper portions of the channels. The dabs, however, seem more inclined to go to greater depths, also. Some fishing experiments from the northern Waddensea (east of Langli Sand) will testify to this. The numbers of plaice and dabs fished were caught by 15 minutes' trawling with the young-plaice trawl (see table 2, compiled by the author from the journals of the Marine-Biological Laboratory).

The investigations carried on for several years in the Danish Waddensea have shown that the quantities of dabs and plaice vary greatly from year to year. JOHANSEN (1922 A)

Table 2.

Date	Depth	Plaice	Dabs
24/11 1937	1.5 m	10	3
	1.0 m	36	7
	2.0 m	24	5
25/11 1937	9.0 m	3	3
30/6 1942	1—1.5 m	318	283
	7—8 m	15	192
10/9 1942	1—2 m	101	85
	5—8 m	2	1
11/9 1942	1.5 m	3	3
	5 m	25	11
	11 m	2	1
22/9 1943	2.5 m	309	36
	9 m	27	399
30/10 1943	1.25 m	208	213
	7 m	74	1395
18/9 1943	1.25 m	79	17
	1.25 m	337	70
	1.25 m	72	24
	5—10 m	7	46
20/6 1946	1 m	90	4
	5—10 m	1	0
24/6 1946	1 m	187	2
	5—10 m	14	3
25/10 1946	1 m	675	202
	5—10 m	6	3

Table 3. Average number of the various age-groups per one hour's haul.

	0	I	II	III
1935—39.....	254	117	43	4
1940—44.....	151	237	95	23
1945.....	211	342	154	33

Table 4. Average size (in cm) of 1-, 2-, and 3-year old plaice in June (for 1939 in July).

	I	II	III
1934.....	8.73	13.52	15.95
1935.....	9.30	13.44	(16.66)
1936.....	8.81	14.75	(17.38)
1937.....	8.75	12.14	—
1938.....	—	—	—
1939.....	11.12 ¹	13.81 ¹	—
1940.....	10.75	16.61	(19.75)
1941.....	10.17	16.36	(20.63)
1942.....	7.85	15.08	(21.75)
1943.....	7.54	11.95	15.34
1944.....	8.48	11.41	(15.00)
1945.....	8.64	11.93	(15.60)

¹ Caught on July 7th.

Parentheses indicate: less than 25 individuals.

showed that these fluctuations may later be reflected in the yield. In 1909 0-group plaice were numerous, and consequently the yields of III- and IV-group plaice in Graadyb in the seasons of 1912—13 and 1913—14 were great. Similarly, an abundance of 0-group plaice in 1912 was succeeded by a profitable fishery of IV-group plaice in 1916—17.

Continuous investigations carried out from the Marine-Biological Laboratory (TÅNING 1943, 1945, and 1947) have shown the remarkable result that in the war-years (1940—45) the numbers of I-, II-, and III-group plaice increased in the Waddensea at the same time as these age-groups showed a decrease in average length and weight. This is illustrated by the figures in tables 3—4 (after TÅNING 1947).

The phenomenon illustrated in the tables is explained by TÅNING as due to the increased pressure from over-crowding of the population of plaice outside the Waddensea owing to the decreasing intensity of fishery during the war, which resulted in a keener competition for food.

Finally, since 1940, examinations of the stomach-contents of the Waddensea plaice have been made at the Marine-Biological Laboratory. These investigations will be dealt with in chapter X (pp. 115—118).

V. The Microfauna of the Bottom.

Not till quite recent years has the marine microfauna of the bottom been subjected to quantitative investigations, but the results arrived at so far are too insufficient to enable us to form a general idea of this faunal element. Publications by the following authors are available: BOUGIS (1946), KROGH and SPÄRCK (1936), MARE (1942), MOORE (1931), PURASJOKI (1945), and REES (1940). As the microfauna of the Waddensea is of great importance for the production, it constitutes a significant part of the investigation recorded in the present paper.

A. The term "microfauna".

The question of how to define the microfauna depends on what use is to be made of this term. Thus WEISS-FOGH (1947—48, p. 240) in his paper on the terrestrial microfauna has given an ecological definition, defining it as "those individuals of the total fauna of the soil which are so small that they are able to move freely in the pores of the earth and are not directly forced to change the structure of the soil by burrowing". According to this definition a number

of animals will under certain circumstances (in soil with fairly big pores) belong to the microfauna, while under other conditions (in soil with minute pores) they will not belong to it.

In the present paper the valuation of the microfauna is made as a supplement to the valuation of the macrofauna according to the method of C. G. J. PETERSEN, so the distinction between the micro- and the macrofauna will depend on the investigation technique employed. The microfauna is here that part of the bottom fauna which will pass through even the most fine-meshed sieves used in the macro-valuation (mesh-width 1 mm), so a special micro-valuation method must be adopted (see chapter II).

The following groups are designated as bottom micro-animals: *Nematodes*, *Copepoda*, *Ostracoda*, *Foraminifera*, etc., and the smallest bottom stages of the macrofauna. However, *Protozoa* (except *Foraminifera*) are not included, and have not been subjected to investigation.

As regards the terminology, there may be some reason to employ the terms proposed by MARE (1942), who operates with the following three groups: 1) microbenthos: (*Protozoa* except *Foraminifera*, bottom Diatoms, and *Bacteria*), 2) meiobenthos (*Nematodes*, *Copepoda*, *Ostracoda*, *Turbellaria*, *Foraminifera*, etc.), and macrobenthos (big organisms). It will be seen that the group which is called meiobenthos by MARE, is identical with that termed microfauna in the present paper. While the latter two of these three groups are subjected to special investigation in the present work, the former group is only treated on the basis of the literature in the chapter on the food of the bottom animals (chapter IX, pp. 110—112).

It should be added here that by the nature of the case there is no sharp distinction between the two groups that are termed microfauna and macrofauna in the present work. Thus it is largely a matter of judgment whether a growing bottom animal should be referred to one or the other group.

In the subjoined treatment of the microfauna of the bottom I have distinguished between: a) the actual microfauna (the animals that remain micro-animals throughout their lifespan) and b) young bottom stages of the macrofauna. In this chapter only the actual microfauna will be treated.

B. Occurrence of individual species or higher systematic groups.

The valuation of the microfauna is based on a total of 585 samples, which is by far the largest number that had been taken in any quantitative investigation. These samples were collected in various localities: on sandy waddens, on soft waddens, and in channels (in shallow water, the places where the young-plaice trawl was used for fishing young fish). More systematic collecting was made on the sand wadden north of Fanø, samples being taken at all seasons of the year at a number of stations from the edge of the wadden (the low-water mark) to the shore (the high-water mark), consequently they represent a cross section of the wadden in its annual variation (see the map in fig. 41, p. 122). The results of these samplings, for *Nematodes*, *Harpacticoidea*, and *Ostracoda*, are represented in figs. 10—13. As to these figures it should be noted: the base line represents the transverse section of the wadden (450 m) with the low-water mark to the left and the high-water mark to the right, and the columns, whose position on the base line corresponds to that of the stations on the wadden, indicate the number of individuals per areal unit. The figures of the ordinate to the left indicate the number of individuals per cm², so, to arrive at the number of individuals per m², they should be multiplied by 10,000. Stations in which only few individuals were taken are marked with a +, and those at which no animals were found are marked with 0.

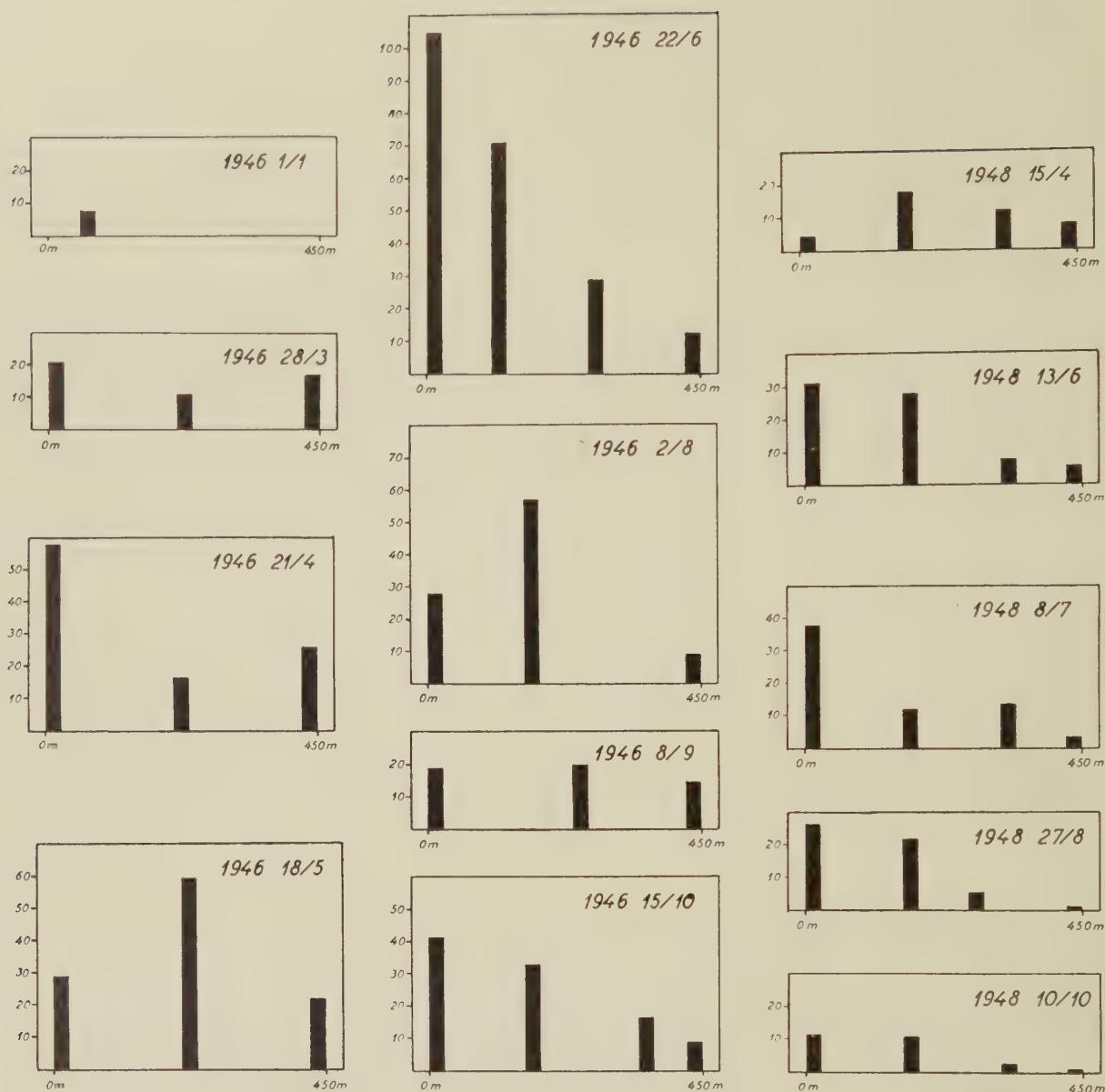


Fig. 10. Numbers of *Nematodes* per cm² in a transverse section of the sand wadden north of Fano at different times of the year.

In the following pages the fairly numerous groups (*Nematodes*, *Copepoda*, *Ostracoda*, and *Foraminifera*) will be treated. The *Turbellaria*, however, which occurred occasionally in a very few specimens, will not be dealt with. It should be added that no *Kinorhyncha* or *Tardigrada* were observed, but possibly they have been overlooked on account of their small size.

1) *Nematodes*.

Determination to species or other systematic group not made. Numbers of individuals in different localities shown in diagrams or figures.

Sand wadden:

The quantity of Nematodes on the sand wadden north of Fanø is shown in the diagrams in fig. 10, which are based on the following samples:

1946: $1/1$ (10 samples of 0.95 cm²), $28/3$ (17 of 0.95 cm²), $21/4$ (18 of 0.95 cm²), $18/5$ (17 of 0.95 cm²), $22/6$ (16 of 0.95 cm²), $2/8$ (19 of 0.95 cm²), $8/9$ (14 of 0.95 cm²), $15/10$ (20 of 0.95 cm²);

1948: $15/4$ (40 of 2.25 cm²), $13/6$ (35 of 2.25 cm²), $8/7$ (40 of 2.25 cm²), $27/8$ (40 of 2.25 cm²), $10/10$ (40 of 2.25 cm²).

Soft wadden:

On the soft wadden at Nordby (Fanø) the following numbers were found in 1946:

$23/6$ 367,000 individuals per m² (7 samples of 0.95 cm²)
 $18/10$ 185,000 — — (5 — — 0.95 —)

Channels:

1945, $2/9$: As an average for four stations east and southeast of Fanø 38,000 individuals per m² (8 samples of 0.95 cm²) were found.

1946, June 20 and 21:

N. and NE. of Fanø 234,000 individuals per m² (11 samples of 2.25 cm²)
 E. of Langli Sand..... 187,000 — — (3 — — 2.25 —)
 Inner Ho Bay 148,000 — — (4 — — 2.25 —)

1946, October 17 and 19:

N. of Fanø..... 83,000 individuals per m² (8 samples of 2.25 cm²)
 NE. of Fanø..... 42,000 — — (4 — — 2.25 —)
 E. of Langli Sand..... 204,000 — — (6 — — 2.25 —)
 Inner Ho Bay 121,000 — — (5 — — 2.25 —)

These figures show that the *Nematodes* are extremely numerous everywhere, both on the waddens and in the channels, at all seasons of the year, though with a minimum in the winter months. They seem, however, to be somewhat more abundant on the waddens than in the channels. Further, they show a decreasing frequency towards the high-water mark.

2) Copepoda.

Several representatives of the group *Harpacticoida* are found on the waddens as well as in the channels, where they constitute a very essential part of the microfauna. The species mentioned below were determined on the basis of material from 1946 and 1947; the determinations were made by ERIK DAHL (Sweden).

Ameira sp.—A few specimens were taken on $14/10$ 1947 in a channel northeast of Fanø and east of Langli Sand.

Amphiascus spp.—Several species were taken in the months of May–December on a soft wadden at Nordby (Fanø) and on the inner part of the wadden north of Fanø, where the bottom is somewhat muddy. Thus they seem to prefer a soft or a mixed bottom. At times they may be of rather frequent occurrence.

Assellopsis intermedia (T. SCOTT).—Taken at all seasons of the year (in January and in the months March–October). Distributed over the whole sand wadden north of Fanø; occurs

in addition on the sand wadden northeast of Fanø and in shallow water in a channel east of Langli Sand. Has not been taken on definitely soft bottom. Varies in frequency at the different times, but was especially frequent in samples from the sand wadden north of Fanø taken in 1946 on the following dates: $1/1$, $2/8$, $10/10$, and $11/12$.

Canuella furcigera G. O. SÆRS.—Found in samples taken at all times of the year both on markedly soft waddens (at Nordby) and on firm sand wadden (north of Fanø), but was not taken in the channels. Especially abundant (sometimes one of the dominant species) in the following samples: Sand wadden north of Fanø $23/6$ 1946, $2/8$ 1946, $11/12$ 1946, $21/7$ 1947, $29/8$ 1947, and soft wadden (at Nordby) $23/6$ 1946.

Cletodidae spp.—Found in samples from March to October taken on sand wadden (north of Fanø) as well as soft wadden (at Nordby). Further found in shallow water in a channel south of Langli Sand. Always taken in small numbers only.

Ectinosoma curticorne BOECK.—Taken some few times in June, July, and October, chiefly on soft bottom. The following finds are at hand: on the soft wadden at Nordby, abundant on $23/6$ 1946 and $22/6$ 1947, but scarce on $8/10$ 1947; abundant on soft bottom in the channel in the interior of Ho Bay on $14/6$ 1947; rather sparse on the outermost part of the sand wadden north of Fanø on $21/7$ 1947.

Ectinosoma spp.—Several species found in small numbers in samples from the soft wadden at Nordby, sand waddens north and northeast of Fanø, and a channel east of Langli Sand from the months June to October.

Ectinosomidae spp.—Taken in samples at all seasons of the year and in all localities (sand wadden north of Fanø, soft wadden at Nordby, channel northeast of Fanø). Numerous in the following samples (in some samples one of the dominants): sand wadden north of Fanø 1946: $18/5$, $2/8$, $8/9$, $10/9$, and $11/12$.

Harpacticus flexus BRADY & ROBERTSON.—Occurs at all times of the year in all kinds of localities (sand wadden north of Fanø, soft wadden at Nordby, and in shallow water in channels east of Langli Sand and northeast of Fanø). Especially numerous (or even dominant) in the following samples: Sand wadden north of Fanø ($1/1$ 1946, $18/5$ 1946, $23/6$ 1946, $2/8$ 1946, $8/9$ and $10/9$ 1946, $11/12$ 1946, $21/7$ 1947, $29/8$ 1947, $10/10$ 1947), channel northeast of Fanø ($14/10$ 1947), channel east of Langli Sand ($14/6$ and $14/10$ 1947).

Laophonte spp. (2 species).—Taken in samples at all seasons of the year on the sand wadden north of Fanø, but never in large numbers. Not taken elsewhere; thus it seems to avoid soft bottom.

Plathychelipus littoralis BRADY.—Only taken on the soft wadden at Nordby ($23/6$ 1946, $18/10$ 1946, $8/10$ 1947), and only in small numbers.

Tachidius brevicornis LILLJEBORG.—Taken in January, March, April, May, June, July, and December. Distributed both on sand wadden (north of Fanø), soft wadden (Nordby), and in channels (east of Langli Sand and northeast of Fanø). Numerous or even dominant in the following samples: sand wadden north of Fanø ($1/1$ 1946, $27/3$ – $28/3$ 1946, $18/5$ 1946, $23/6$ 1946, $11/12$ 1946, $16/6$ 1947); channel northeast of Fanø ($16/6$ 1947).

Tachidius littoralis POPPE.—Taken in June and October, only on soft bottom (soft wadden at Nordby, channel in the interior of Ho Bay). Numerous and dominant in the following samples: Soft wadden at Nordby ($22/6$ 1947, $8/10$ 1947), interior of Ho Bay ($14/6$ 1947).

From these data the following information concerning the distribution of the *Harpacticoida* on the different kinds of bottom can be deduced:

- a) Some species occur exclusively or chiefly on sandy bottom: *Assellopsis intermedia*, *Harpacticus flexus*, *Laophonte* spp. (2 species), *Tachidius brevicornis*.
- b) Some species occur exclusively or chiefly on soft bottom: *Amphiascus* spp., *Ectinosoma curticorne*, *Plathychelipus littoralis*, *Tachidius littoralis*.
- c) Evenly distributed over soft bottom and sandy bottom: *Canuella furcigera*.

Representatives of the *Cletodidae* and the *Ectonosomidae* are found both on sandy and on soft bottom, but since they were not determined specifically, nothing can be stated about the distribution of the species.

Thus there seems to be a certain difference in the specific composition of the *Harpacticoida* on soft bottom and on sandy bottom within the area investigated. It should be pointed out that a single genus occurs with two different mutually vicarious species on the two types of bottom, viz. *Tachidius brevicornis* (sandy bottom) and *T. littoralis* (soft bottom).

The investigations on the sand wadden north of Fanø have revealed an interesting annual variation in the composition of the species. In samples from 1946 from the months of January, March, April, May, and June *Tachidius brevicornis* is dominant, and in the samples from the two last-mentioned months it is present in large numbers. In the later samples, from August and September, it is absent or very scarce; but in the December-samples it is again among the dominants. In 1947 it was dominant in the samples from June, but in the following samples from July, August, and October it was either absent or present in very small numbers. Thus the species has its main occurrence in the winter, spring, and early summer, when it finally culminates, and is then entirely replaced by other species. *Harpacticus flexus* was found as dominant in 1946 in samples from January, May, June, August, September, and December, and in 1947 in samples from July, August, and October; in the samples from the other months it was sparse or absent. *Canuella furcigera* has a similar occurrence to that of *Harpacticus flexus*, though its earliest occurrence as dominant was observed in the month of June (1946). Other species, also, may occasionally occur as dominants.

Summing up the data on the annual variation and the species composition given above, we obtain the following picture: From winter to mid-summer *Tachidius brevicornis* occurs as dominant, culminating in May—June, after which time it is entirely ousted by other dominant species, of which *Harpacticus flexus* is the most constant, occurring as dominant in the summer and autumn months till well into the winter.

The diagrams (figs. ¹¹ ~~13~~ and ¹² ~~14~~) and the figures given below will serve to show the quantitative occurrence of the *Harpacticoida* in the different localities. Here the individual species or groups are not taken into consideration, but only the *Harpacticoida* as a whole:

Sand waddens:

Fig. 11 shows the numbers of *Harpacticoida* on the sand wadden northeast of Fanø in 1942, and fig. 12 the figures for the wadden north of Fanø in the years 1946, 1947, and 1948. Fig. 11 is based on 25 "skimmer" samples of 25 cm², and fig. 12 on the following samples:



Fig. 11. Numbers of *Harpacticoida* per cm² on the sand wadden northeast of Fanø (near the low-water mark) in 1942.

1946: $^1/1$ (10 samples of 0.95 cm²), $^{28}/3$ (17 of 0.95 cm²), $^{21}/4$ (18 of 0.95 cm²), $^{18}/5$ (17 of 0.95 cm²), $^{22}/6$ (16 of 0.95 cm²), $^2/8$ (19 of 0.95 cm²), $^8/9$ (14 of 0.95 cm²), $^{15}/10$ (20 of 0.95 cm²), $^{11}/12$ (14 skimmer-samples of 25 cm²).
 1947: $^{26}/6$ (24 of 0.95 cm²), $^{18}/6$ (32 of 0.95 cm²), $^{21}/7$ (24 of 0.95 cm²), $^{29}/8$ (24 of 0.95 cm²), $^{10}/10$ (32 of 2.25 cm²).
 1948: $^{15}/4$ (40 of 2.25 cm²), $^{13}/6$ (35 of 2.25 cm²), $^8/7$ (40 of 2.25 cm²), $^{27}/8$ (40 of 2.25 cm²), $^{10}/10$ (40 of 2.25 cm²).

Soft wadden:

On the soft wadden at Nordby the following numbers were found in 1946:

$^{23}/6$	389,000	individuals	per m ²	(7 samples of 0.95 cm ²)
$^{18}/10$	111,000	—	—	(5 — — 0.95 —)

In the same place the following numbers were found in 1947:

$^{22}/6$	253,000	individuals	per m ²	(8 samples of 0.95 cm ²)
$^{20}/7$	13,000	—	—	(6 — — 0.95 —)
$^{28}/8$	15,000	—	—	(8 — — 0.95 —)
$^8/10$	50,000	—	—	(9 — — 2.25 —)

Channels:

1945, $^2/9$: As an average of four stations east and south of the southernmost point of Fanø 58,000 individuals per m² were found (8 samples of 0.95 cm²).

1946, $^{20}/6$ — $^{21}/6$:

N. and NE. of Fanø	318,000	individuals	per m ²	(11 samples of 2.25 cm ²)
E. of Langli Sand.....	211,700	—	—	(3 — — 2.25 —)
Inner Ho Bay	18,700	—	—	(4 — — 2.25 —)

1946, $^{17}/10$ — $^{19}/10$:

N. and NE. of Fanø	12,100	individuals	per m ²	(12 samples of 2.25 cm ²)
E. of Langli Sand.....	62,000	—	—	(6 — — 2.25 —)
Inner Ho Bay	6,100	—	—	(5 — — 2.25 —)

1947, $^{14}/6$ — $^{16}/6$:

N. and NE. of Fanø	13,000	individuals	per m ²	(4 samples of 2.25 cm ²)
E. of Langli Sand.....	62,000	—	—	(3 — — 2.25 —)
Inner Ho Bay.....	400,000	—	—	(6 — — 2.25 —)

1947, $^{14}/10$ — $^{15}/10$:

N. of Fanø.....	23,000	individuals	per m ²	(4 samples of 2.25 cm ²)
NE. of Fanø.....	7,000	—	—	(4 — — 2.25 —)
E. of Langli Sand.....	41,000	—	—	(8 — — 2.25 —)
Inner Ho Bay.....	3,000	—	—	(4 — — 2.25 —)

1948, $^{11}/6$ — $^{15}/6$:

N. of Fanø.....	31,000	individuals	per m ²	(6 samples of 2.25 cm ²)
E. of Langli Sand.....	32,600	—	—	(6 — — 2.25 —)
Inner Ho Bay	28,900	—	—	(6 — — 2.25 —)

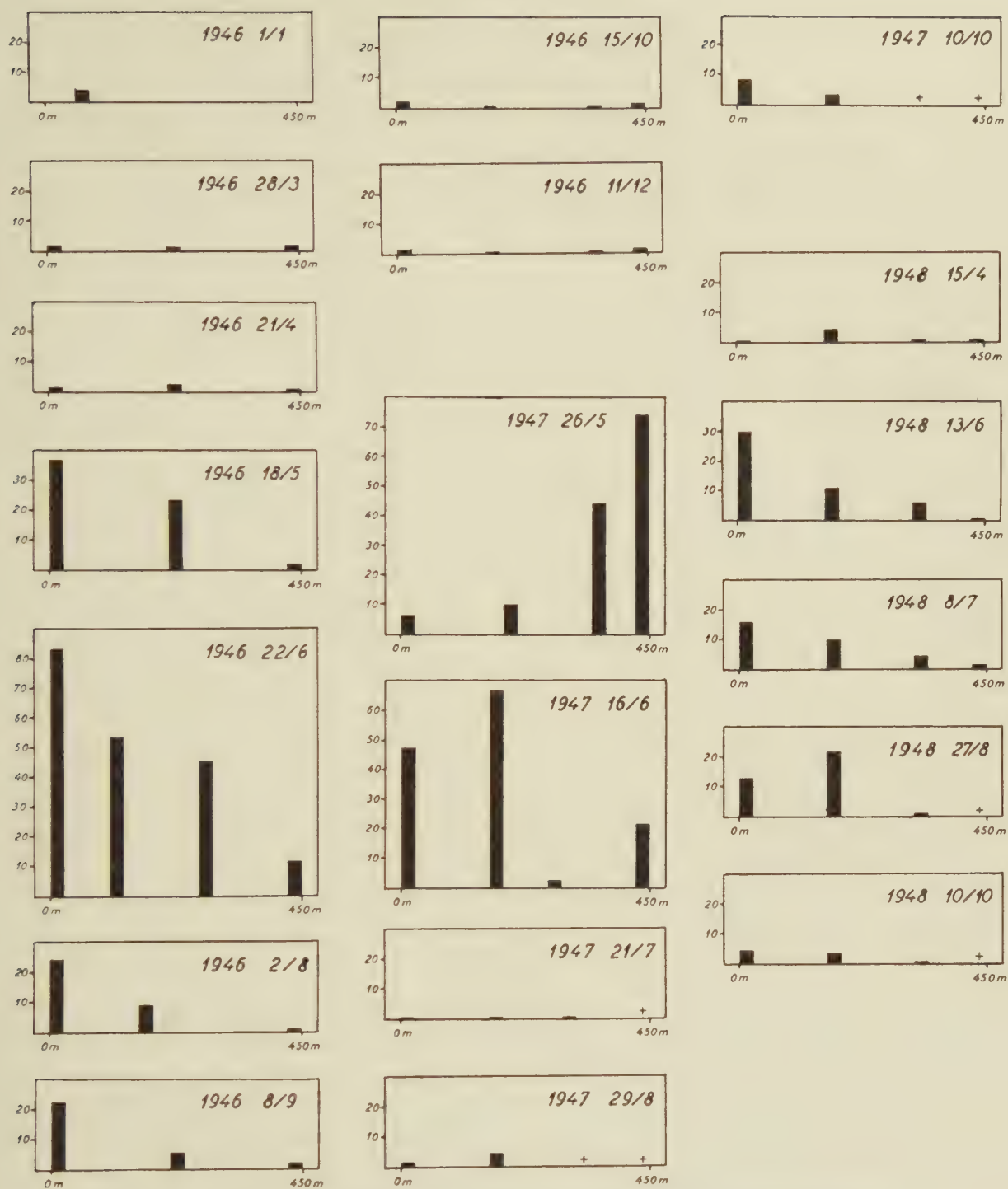


Fig. 12. Numbers of *Harpacticoidea* per cm² in a transverse section of the sand wadden north of Fano at different times of the year.

The following facts can be deduced from the diagrams and the figures:

The stocks of *Harpacticoidea* are generally more abundant on the waddens than in the channels; but both on the waddens and in the channels exceedingly numerous stocks may be met with. Further it will be seen that there is a rather considerable seasonal variation, as will especially appear from the investigations carried out regularly on the sand waddens north and northeast of Fanø. From a minimum in the winter and the early spring, the number increases to a maximum in the month of June, to be succeeded by a distinct fall (especially marked in the series of samples from 1942 and 1947). In the late summer or the autumn there may be a slight increase of the number again. Diagrams from the sample line north of Fanø show that the largest numbers generally occur on the outer part of the wadden, whence the numbers decrease towards the high-water mark; however, there are several deviations from this rule.

For comparison of the numbers in the different localities (waddens and channels) and at different seasons of the year, a few figures typical of the material given above are here submitted:

Waddens	{	The sand wadden N. of Fanø: (170 m from low-water mark)	{	Maximum 674,000/m ² (¹⁸ / ₆ 1947)
				Minimum 4,000/m ² (¹⁵ / ₁₀ 1946)
	{	The soft wadden at Nordby:	{	Maximum 389,000/m ² (²³ / ₆ 1946)
				Minimum 13,000/m ² (²⁰ / ₇ 1947)
Channels	{	Interior of Ho Bay:	{	Maximum 400,000/m ² (June 1947)
				Minimum 6,100/m ² (October 1946)
	{	N. and NE. of Fanø:	{	Maximum 318,000/m ² (June 1946)
				Minimum 12,100/m ² (October 1946)

3) *Ostracoda*.

According to identifications made by Mr. B. DAMSTEDT-CHRISTENSEN, the following species were found on the sand wadden north of Fanø on June 22, 1946: *Cytherois arenicola* KLIE, *C. fisheri* G. O. SARS, *Cytherura sella* G. O. SARS, *Leptocythere baltica* KLIE, *L. pellucida* (BAIRD), *Loxochonca pusilla* (BRADY and ROBERTSON), and an undetermined Ostracod species.

The following diagrams and figures will illustrate the quantitative occurrence of the *Ostracoda* in the Waddensea:

Sand waddens:

The result of the collections made periodically on the sand wadden north of Fanø in 1946, 1947, and 1948 are shown in the diagrams in fig. 13, which are based on the following samples:

1946: ¹/₁ (10 samples of 0.95 cm²), ²⁸/₃ (17 of 0.95 cm²), ²¹/₄ (18 of 0.95 cm²), ¹⁸/₅ (18 of 0.95 cm²), ²²/₆ (17 of 0.95 cm²), ²/₈ (19 of 0.95 cm²), ⁸/₉ (14 of 0.95 cm²), ¹⁵/₁₀ (20 of 0.95 cm²).

1947: ²⁶/₅ (24 of 0.95 cm²), ¹⁶/₆ (32 of 0.95 cm²), ²¹/₇ (24 of 0.95 cm²), ²⁹/₈ (24 of 0.95 cm²), ⁹/₁₀ (32 of 2.25 cm²).

1948: ¹⁵/₄ (40 of 2.25 cm²), ¹³/₆ (35 of 2.25 cm²), ⁸/₇ (40 of 2.25 cm²), ²⁷/₈ (40 of 2.25 cm²), ¹⁰/₁₀ (40 of 2.25 cm²).

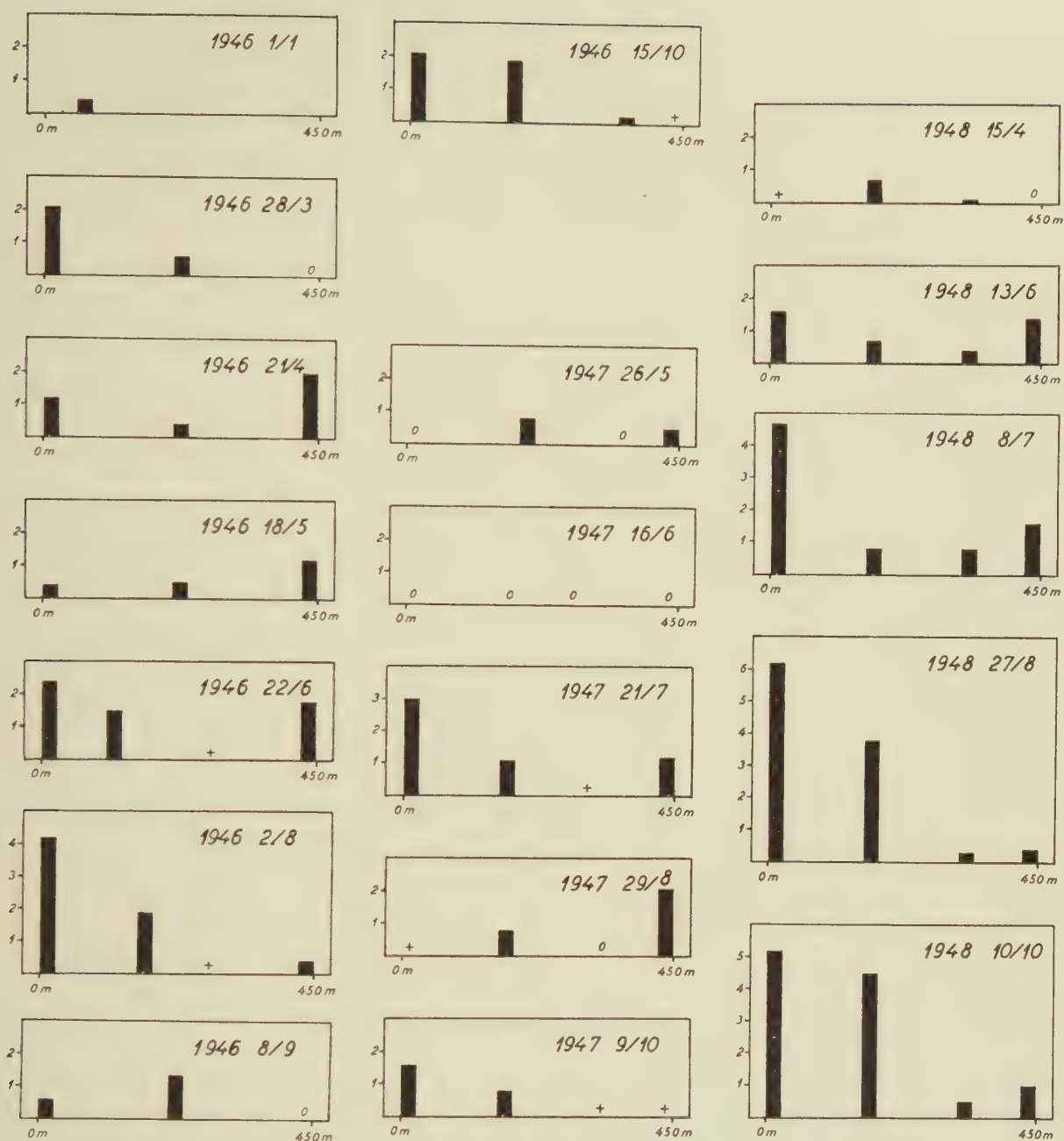


Fig. 13. Numbers of *Ostracoda* per cm² in a transverse section of the sand wadden north of Fano at different times of the year.

The sand wadden northeast of Fano gave the following figures:

1946, ¹⁸ /10.....	8,000	per m ²	(5	samples of 0.95 cm ²)
1947, ²⁰ /7.....	53,000	—	(6	0.95 —)
²⁸ /8.....	17,000	—	(8	0.95 —)
⁹ /10.....	2,000	—	(9	0.95 —)

Soft wadden (at Nordby):

1946, $^{23}/_6$	12,000	per m ²	(7 samples of 0.95 cm ²)
$^{18}/_{10}$	4,000	—	(5 — — 0.95 —)
1947, $^{22}/_6$	5,000	—	(6 — — 0.95 —)
$^{20}/_7$	5,000	—	(6 — — 0.95 —)
$^{28}/_8$	few spec.	—	(8 — — 0.95 —)
$^8/_{10}$	9,000	—	(9 — — 0.95 —)

Channels (trawl stations):

1945, $^2/_9$: As an average for four stations east and south of Fanø only very few specimens were found (8 samples of 0.95 cm²).

1946, $^{20}/_6$ — $^{21}/_6$:

N. and NE. of Fanø	3,000	individuals per m ²	(11 samples of 2.25 cm ²)
E. of Langli Sand	a few	— —	(3 — — 2.25 —)
Interior of Ho Bay	a few	— —	(4 — — 2.25 —)

1946, $^{17}/_{10}$ — $^{19}/_{10}$:

N. of Fanø	no	individuals per m ²	(8 samples of 2.25 cm ²)
E. of Langli Sand	few	— —	(6 — — 2.25 —)
Interior of Ho Bay	few	— —	(5 — — 2.25 —)

1947, $^{14}/_6$ — $^{16}/_6$:

N. of Fanø	no	individuals per m ²	(3 samples of 2.25 cm ²)
E. of Langli Sand	no	— —	(3 — — 2.25 —)
Interior of Ho Bay	few	— —	(6 — — 2.25 —)

1947, $^{14}/_{10}$ — $^{15}/_{10}$:

N. and NE. of Fanø	no	individuals per m ²	(8 samples of 2.25 cm ²)
E. of Langli Sand	few	— —	(7 — — 2.25 —)
Ho Bay off Marbæk	few	— —	(3 — — 2.25 —)
Interior of Ho Bay	no	— —	(4 — — 2.25 —)

1948, $^{11}/_6$ — $^{15}/_6$:

N. and NE. of Fanø	few	individuals per m ²	(6 samples of 2.25 cm ²)
E. of Langli Sand	6,000	— —	(6 — — 2.25 —)
Interior of Ho Bay	13,000	— —	(6 — — 2.25 —)

These diagrams and figures show with great distinctness that the *Ostracoda* occur in much smaller numbers than both the *Nematodes* and the *Harpacticoidea*. The largest numbers are found on the waddens, especially on the sand waddens (maximum number found was 52,000 per m² on the outermost part of the sand wadden north of Fanø, $^{10}/_{10}$ 1948). In most cases the numbers were larger on the outer parts of the waddens (nearest the low-water mark) than on the inner parts (nearest the high-water mark).

4) *Foraminifera*.

As the *Foraminifera* do not seem to be of importance as food for the young plaice, and as they are much more difficult to separate from the samples than the other microfaunal animals, because the washing method cannot be employed, they were counted in only a very few cases.

The diagram in fig. 14 shows the numbers for some samples taken on the sand wadden north of Fanø on May 18, 1946. The numbers for the outer part of the wadden are fairly high, but there is a rapid decline towards the high-water mark.

C. Features of the reproduction biology of the microfauna.

Concerning the question as to how rapidly and effectively the microfauna is replaced, only very sporadic data can be given. What can be deduced from the literature about this question will be recorded below.

About the marine *Nematodes* no information is available, as far as I know. As to the terrestrial *Nematodes* OVERGAARD NIELSEN (1949, pp. 93—94) states that at a temperature of ca. 15° C. an egg will as a rule take about 20 days to develop into an adult egg-producing female. If the marine *Nematodes* have a similar time of development, we may count upon several generations a year.

As to the *Harpacticoidea*, a few data are recorded in the literature. The most thoroughly investigated form is *Tisbe furcata* (BAIRD), a cosmopolitan bottom form, which occurs as near the area of investigation as at Sylt (see LANG, 1948). At the Scripps Institution (California) JOHNSON, MARTIN, and OLSEN (1948) studied the life cycle of some individuals at a temperature of 17—18° C. in some aquarium experiments. The experiments showed that the average life-time of a female is 40—50 days, during which period it generally spawns nine times, producing, on an average, a total of 513 eggs. Of these, 80 per cent. or 410 individuals survive till the adult stage, and about one-third of these are females, i. e. 133 individuals. Generally there are 25 days between two generations.—From these figures the authors calculated that in the course of 100 days a single female produces four generations numbering in all 1 billion and 55 million individuals, provided, of course, no persecution by enemies takes place. With this enormous reproduction intensity the mortality in nature must necessarily be very high.

A. G. NICOLS (1935) states that every female individual of *Longipedia coronata* CLAUS and *L. minor* T. & A. SCOTT spawns several times. FRASER (1936), in aquarium experiments at Hull, found that *Tigriopus fulvus* (FISHER) takes two months to reach the adult stage, while TSEN-HWANG SHAW (1938) states that in the Pacific the same species takes only one month to reach that stage.

These scattered data would seem to suggest that commonly every female spawns several times, and that several generations are produced in the course of a year.

No experiments similar to those mentioned above have been made in the Danish Wadden-sea. However, in the material of *Harpacticoidea* I have computed the percentage quantity of egg-bearing individuals of the total stock of all the species. For the sand wadden north of Fanø these percentages were as follows:

1942: $\frac{15}{3}$ (30 0/0), $\frac{7}{6}$ (20 0/0), $\frac{30}{6}$ (25 0/0), $\frac{16}{7}$ (25—30 0/0), $\frac{31}{7}$ (0 0/0), $\frac{21}{8}$ (19 0/0), $\frac{6}{10}$ (5 0/0), $\frac{24}{11}$ (ca. 0.1 0/0).
 1946: $\frac{1}{1}$ (ca. 8 0/0), $\frac{28}{3}$ (28 0/0), $\frac{21}{4}$ (31 0/0), $\frac{18}{5}$ (16 0/0), $\frac{22}{6}$ (8 0/0), $\frac{2}{8}$ (20 0/0), $\frac{8}{9}$ (9 0/0), $\frac{15}{10}$ (4 0/0).
 1947: $\frac{16}{6}$ (16 0/0), $\frac{21}{7}$ (18 0/0), $\frac{29}{8}$ (9 0/0), $\frac{10}{10}$ (3 0/0).

These percentages, which can be regarded as an expression of the reproduction intensity of the stock, show high values for the period March—August. As the individual species (those

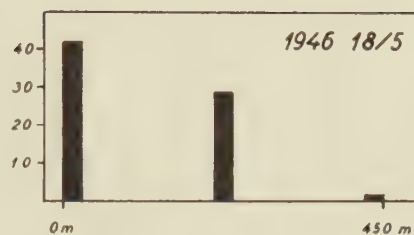


Fig. 14. Number of *Foraminifera* per cm² in a transverse section of the sand wadden north of Fanø on 18/5 1946.

of numerical importance) occur over a period of several months, it may be regarded as probable that they produce several generations a year.

The reproduction intensity of the *Ostracoda*, according to the investigations made by ELOFSON (1941), seems to be very low as compared with that of the *Harpacticoidea*. The eggs are, as a rule, carried for a long time (in some cases for several months), before the larvae are hatched, and the development proper from the newly-hatched egg to the adult stage lasts, for the bottom forms, ca. 2 years or more. As the *Ostracoda* are probably just as much pursued by enemies as the *Harpacticoidea* (like these, they are found in the stomach contents of quite young fish), the low reproduction intensity may be regarded as the cause of the much sparser representation of the *Ostracoda* than of the *Harpacticoidea* in the bottom samples.

D. General characterisation of the microfauna. Comparison with other regions.

The present study of the bottom microfauna of the Waddensea has shown that (apart from the *Foraminifera*) the *Nematodes* and the *Harpacticoidea* are by far the dominant groups among the actual microfaunal animals, while the *Ostracoda* play a more subordinate part, and the *Turbellaria* are of very sparse occurrence and were only found in a few samples.

The Waddensea—as compared with other areas investigated—harbours a particularly rich microfauna. The richest samples from the Waddensea were taken on the sand wadden north of Fanø on June 22, 1946. The largest numbers were found at the station on the extreme outer part of the wadden:

<i>Nematodes</i>	1,048,000	individuals	per m ²
<i>Harpacticoidea</i>	837,000	—	—
<i>Ostracoda</i>	24,000	—	—

For comparison the largest numbers found for the same animal groups by the various authors will be given below:

	<i>Nematodes</i> pr. m ²	<i>Copepoda</i> pr. m ²	<i>Ostracoda</i> pr. m ²
REES 1940 (tidal area in Bristol Channel).....	10,400,000	500,000	790,000
MOORE 1931 (Loch Head, Clyde Sea area, 24 m)	251,500	69,700	12,500
MARE 1942 (at Plymouth, 45 m)	116,000	32,000	6,000
KROGH and SPÄRCK 1936 (the Sound, 17 m)	87,000	14,500	1,600
BOUGIS 1946 (Lion Bay, 200 m)	888,000	136,000	19,000
PURASJOKI 1945 (Tværminne, Finland, salinity 0.5 ‰)	58,120	4,840	37,360

From these figures it appears that the richest bottom microfauna is found in tidal areas, the figures for such localities in the Danish Waddensea and in the Bristol Channel being noticeably higher than for the other localities. It should be added that the area investigated by PURASJOKI differs from the rest by a low salinity.

A number of investigations have been made for the purpose of finding out how far down in the bottom the various constituents of the microfauna occur. Investigations carried out by MOORE (1931), KROGH and SPÄRCK (1936), REES (1940), MARE (1942), and BOUGIS (1946) agree in showing that by far the greater part of the *Harpacticoidea* and *Ostracoda* are found in the uppermost centimetre of the bottom, while the *Nematodes* are numerous several centi-

metres down. In the Waddensea the Nematodes are likewise found at greater depths than the other groups; but by far the greater number of all the three groups occur in the uppermost centimetre, as shown by the figures given below. The contents of five samples (each covering 2.25 cm²) taken on the sand wadden north of Fanø on June 13, 1948, showed the following distribution:

	<i>Nematodes</i>	<i>Harpacticoidea</i>	<i>Ostracoda</i>
0—1 cm.	298	117	7
1—2 —	30	11	2
2—4 —	23	6	2
4—6 —	6	0	0

The contents of 5 samples (each of 2.25 cm²) taken in the same locality on July 1, 1949, showed the following vertical distribution:

	<i>Nematodes</i>	<i>Harpacticoidea</i>	<i>Ostracoda</i>
0—1 cm.	292	394	15
1—2 —	81	40	1
2—3 —	45	15	0
3—4 —	67	1	1
4—5 —	4	0	0
5—6 —	18	0	0

From these figures it appears that if samples are taken in the uppermost two centimetres of the wad bottom, the great majority of *Harpacticoidea* and *Ostracoda* will be secured, and that if samples are taken down to 4 cm, the greater number of the *Nematodes* will be secured, also.

To conclude this chapter a few remarks will be offered on the differences, erected by REMANE (1933), between the different biocoenoses. REMANE (l. c.) shows that the various biocoenoses differ not only in species number and species composition, but also in form characters and function characters. It is shown that species living on sandy bottom are generally more slender and longer than those found on a muddy bottom, and the difference is given by an average length index for the different localities. Both REMANE (l. c.) and later KUNZ (1935) give such length indices for sand, mud, and the phytal region in the Bay of Kiel; but since these are calculated as averages of the species found without considering their quantitative occurrence, there is a great danger that the figures may be somewhat misleading. The problem is discussed by ERIK DAHL (1948, pp. 152—153), and as an example showing how dangerous generalisations in this field may be, he mentions that in a certain locality the dominant species at one season was a Harpacticid species with one length index, while another species with a different length index dominated at another season of the year.

A consideration of the conditions in the Waddensea shows that there seems to be no conspicuous morphological differences between the microfauna of the sand waddens and that of the mud waddens. As to the Harpacticoidea it has been shown that the majority of species occur in both kinds of localities, but in different quantitative proportions, and in addition it has been shown that different species dominate at the different times of the year. Hence it seems obvious that if different morphological features are employed to characterise the different biocoenoses, the investigation must be based on quantitative collecting of samples, and

these should be taken at different times of the year. However interesting and inspiring REMANE's and KUNZ's works are, the results hitherto arrived at should be accepted with a certain reserve.

Questions regarding the food of the microfauna are treated in chapter IX (pp. 110—112), while the consumers of the microfauna are dealt with in chapter X (pp. 112—119).

VI. The Macrofaunal Species of the Bottom and their Occurrence.

The bottom fauna of the Frisian Waddensea has been described in several publications: 1) Dutch: REDEKE (1922), HOFKER (1930); 2) German: MÖBIUS (1893), HAGMEIER and KÄNDLER (1927), WOHLLENBERG (1937), LINKE (1939); 3) Danish: WESENBERG-LUND (1904), MORTENSEN (1922), THAMDRUP (1935), and SMIDT (1944 B).

A. Survey of the faunal areas.

In a description of the bottom fauna of the Waddensea it will be natural to treat separately: a) the bottom fauna of the waddens, and b) the bottom fauna of the channels. The faunal constituents of these areas may be subdivided as follows:

a) bottom fauna of the waddens	I) infauna:	<i>Macoma baltica</i> community
	II) epifauna:	1) sessile: { <i>Zostera</i> epifauna
		2) vagile: { <i>Mytilus</i> epifauna
b) bottom fauna of the channels:	I) infauna:	In part a <i>Macoma baltica</i> community.
	II) epifauna:	{ <i>Mytilus</i> epifauna
		1) sessile: { <i>Ostrea</i> epifauna
		{ <i>Sabellaria</i> epifauna
	2) vagile:	{ true benthos
		{ nekto-benthos

a) The bottom fauna of the waddens:

The fauna living on the waddens is a *Macoma baltica* community, which throughout the whole area (the Danish, the German, and the Dutch Waddensea) shows great uniformity, but with local variations according to the varying levels, the quality of the bottom, etc. Quite corresponding communities are met with in other places, also, along the coasts of the North Sea, thus in the British estuaries.

I) By far the greater part of the bottom fauna of the waddens is an infauna, the most important species of which are: *Polychaeta*: *Phyllodoce maculata*, *Eteone longa*, *Nereis diversicolor*, *Nephtys hombergi*, *Scoloplos armiger*, *Pygospio elegans*, *Polydora ligni* (= *ciliata*?), *Heteromastus filiformis*, *Capitella capitata*, *Arenicola marina*; — *Lamellibranchiata*: *Cardium edule*, *Macoma baltica*, *Mya arenaria*, *Scrobicularia plana*; — *Gastropoda*: *Hydrobia ulvae*; — *Crustacea*: *Bathyporeia pilosa*, *Corophium volutator*.—In addition to these species, a number of less frequent species occur, some of which are only casual visitors.

II) In addition to the infauna, the waddens also harbour an epifauna, comprising both sessile and vagile animals. The most important of the sessile epifaunal animals is *Mytilus edulis*, which is especially abundant in *Mytilus* banks in certain places on the outer part of the waddens; but besides these, scattered *Mytilus* clumps occur over the greater part of the waddens. Attached to the *Mytilus* shells—as well as to stones and other fixed objects—are *Hydroidea*, *Membranipora reticulum*, and two species of *Balanus*. Farther towards the interior of the waddens, growths of *Zostera*, with which an epifauna of *Hydroidea*, etc., is associated, occur in several places. The vagile epifauna is primarily represented by *Littorina littorea*, which is found throughout the greater parts of the waddens; further, a few *Eupagurus bernhardus*, *Carcinus maenas*, and other species occur.

b) The bottom fauna of the channels.

While the infauna plays by far the dominant role on the waddens, the fauna of the channels is to a much greater extent an epifauna. In the more shallow-watered parts of the channels the same animals are largely met with as on the waddens, while in deeper water quite different species dominate, as the deeper channel fauna must be regarded as a thinned out offshoot of the bottom fauna of the North Sea, which will therefore be briefly mentioned.

According to BLEGVAD (1922) and HAGMEIER (1925), the following communities are found in the adjoining parts of the North Sea: 1) A *Syndosmya alba* community is distributed in the inner part of the Heligoland Bay and extends in a very narrow zone northward along the North Frisian Islands as far as Skallingen. Outside this community—north and west of the Heligoland Bay—occurs 2) a *Venus gallina* community, and outside this, again, 3) an *Amphiura filiformis* community. These communities are further of interest because larvae of a considerable number of bottom animals which do not occur as adults in the inner Waddensea, are carried with the tidal current into this area (see further chapter VIII, pp. 107—108).

The bottom fauna of the channels has especially been studied in the northern part of the German Waddensea by HAGMEIER and KÄNDLER (1927). On the basis of this and other investigations the following survey may be given:

I) The infauna of the channels in the more shallow-watered areas (from the low-water mark to a depth of ca. 2 m), where the bottom is of the same quality as on the waddens, consists of the character animals of the *Macoma baltica* community: *Nereis diversicolor*, *Scoloplos armiger*, *Cardium edule*, *Macoma baltica*, *Mya arenaria*, *Hydrobia ulvae*, and *Corophium volutator*.—In deeper water the following species are met with: *Magelona papillicornis*, *Ophelia limacina*, *Pectinaria koreni*, *Lanice conchilega*, and—according to HAGMEIER and KÄNDLER (l. c.)—*Tapes pullastra*, *Syndosmya alba*, and *Amphipholis squamata*.—A species like *Nephtys hombergi* is native both to the waddens and in the channels. Some of the species associated with the channels may in addition occur in small numbers on the outer part of the waddens; this is the case with *Pectinaria koreni*, *Lanice conchilega*, and *Magelona papillicornis*. Other species occur only at great depths, e. g. *Ophelia limacina*.

II) The epifauna may naturally be divided into the sessile and the vagile epifauna.

1) The sessile epifauna, according to HAGMEIER and KÄNDLER (1927), occurs especially in three communities, each of which has its particular depth zone. In quite shallow water—just below the low-water mark—there occur in places dense *Mytilus* banks, a continuation of those found on the outer parts of the waddens. From the depth zone between the low-water mark and a depth of 6—8 m, HAGMEIER and KÄNDLER (l. c.) record the occurrence of *Ostrea*

banks, whose stocks of living *Ostrea*, however, are extremely sparse. The *Ostrea* banks occurring in the Danish Waddensea had been destroyed already at the beginning of the last century (KROYER 1837); i. a. the remains (empty shells) of a destroyed *Ostrea* bank are still found at the northeastern part of Fanø. Of the sessile epifaunal animals associated with the *Ostrea* banks, the following, which occur in the channels wherever the depth and bottom are suitable, may be mentioned, in addition to the few living *Ostrea edulis*: *Spongia* (probably with a preponderance of *Halicondria panicea*), *Hydroidea* (especially *Hydrallmania falcata* and *Sertularia cupressina*), *Pomatoceros triqueter*, and various species of *Balanus*. Fairly common on Lamelli-branch shells in the channels is *Sagartiogeton undatus*, which also occurs on *Cardium* shells on the waddens (THAMDRUP 1935). The 3rd epifaunal community—the *Sabellaria* community—according to HAGMEIER and KÄNDLER (l. c.) occurs in the depth zone between ca. 8 and ca. 18 m. This epifauna is characterised by *Sabellaria spinulosa*, which forms large blocks of sand tubes. As associate species of this community, various *Hydroidea* and the tube-building *Corophium bonelli* are recorded. The *Sabellaria* epifauna is probably distributed wherever the depth and bottom are suitable (the slopes of the deep portions of the channels); the community occurs i. a. in Graadyb, where, however, it has only been very slightly studied.

2) The vagile epifauna plays a very important part in the channels. In describing this fauna it will be practical to distinguish between true benthic animals and nekto-benthos.—a) True benthos consists of the animals which live constantly on the bottom. They include a number of species which occur with greater or less frequency in most places in the channels, but are only exceptionally met with on the waddens: *Buccinum undatum*, *Eupagurus bernhardus*, *Carcinus maenas*, *Asterias rubens*, and *Psammechinus miliaris*. Of these, *Carcinus maenas* is generally met with in enormous numbers in the rather shallow-watered areas. On the waddens the adult *Carcinus* individuals are only occasionally met with, while the 0-group individuals are numerous here in the summer months. Possibly, however, a great many big *Carcinus* individuals migrate some distance in over the waddens at high-tide. *Eupagurus bernhardus*, too, is numerous in the channels, but occurs not by far in such great quantities as *Carcinus*. Not rarely a few individuals are encountered on the waddens.—b) The nekto-benthos includes such species as occur both along the bottom and higher up in the free water masses. To this group may be referred *Crangon vulgaris* and *Mysis flexuosa*, the former of which is chiefly a bottom-animal, while the latter is mainly free-swimming. *Crangon vulgaris* is found in enormous quantities in the shallow-watered parts of the channels, where it plays an important part as fish-food. A great many migrate with the flood-tide across the waddens, and no small number remain there at low-water, burrowing in the bottom. *Mysis flexuosa* is likewise abundant in the channels and, like *Crangon*, it is valuable as fish-food. At ebb-tide a number of *Mysis* may be found in pools on the waddens (THAMDRUP 1935, and author's own observations).

B. List of species.

The subjoined list comprises the species that have been found in the Danish Waddensea. To cover the whole Frisian Waddensea, this list must be supplemented by the species recorded in the literature mentioned above (p. 34).

As to each species, it is briefly stated what is known about its occurrence within the area; but no figures are given for the quantitative occurrence of the species. Such figures will be given for the most important species in chapters VII and XI. If not otherwise stated, the

species was found by the author. Those marked with an × have previously been published from the Danish Waddensea.

Spongiaria:

Spongia occur in large quantities in many places in the channels. According to HAGMEIER and KÄNDLER (1927), *Halicondria panicea* PALLAS is by far the most frequent.

Cnidaria:

× *Sagartiogeton undatus* (O. F. MÜLLER) is found on stones and Lamellibranch shells, mainly in channels, but also on waddens. On a wadden area at Skallingen THAMDRUP (1935) found it attached to the back of living *Cardium*.

Hormathia digitata (O. F. MÜLLER). Some few individuals were taken off the harbour of Esbjerg at a depth of ca. 7—8 m.

Laomedea dichotoma (L.). Taken on *Zostera* on a sand wadden near Esbjerg. Probably distributed throughout the whole Waddensea.

Laomedea loveni ALLMAN. Taken in the harbour at Esbjerg. Probably widely distributed in the Waddensea.

Sertularia cupressina L. Of common occurrence in the channels.

Calicella syringa (L.)?. Taken in a channel south of Esbjerg.

Hydractinia echinata FLEMING. Occurs on snail shells inhabited by *Eupagurus*.

Nemertini:

A few individuals found on sand waddens and waddens with a mixed bottom.

Oligochaeta:

Peloscolex benedeni UDER. and *Tubifex costatus* CLAP. Both species occur on all types of waddens. Most frequently they are found on the higher-lying wadden areas (notably nearest the shore), where they may be exceedingly numerous.

Polychaeta:

Harmothoe imbricata (L.). A few individuals were taken on the outer part of a sand wadden (north of Fanø) and in channels.

Gattyana cirrosa (PALLAS). Some few individuals were taken on a sand wadden (north of Fanø) and in a channel (east of Langli Sand).

Lepidonotus squamatus (L.). A few individuals were taken in channels (south of Esbjerg and east of Langli Sand).

Phyllodoce maculata ØRSTED. Of scattered occurrence on all types of waddens throughout the whole area. A few specimens were taken in channels.

Eteone longa FABR. Of the same distribution as the preceding species, but somewhat commoner.

× *Nereis diversicolor* O. F. MÜLLER. Commonly distributed on all types of waddens, but seems especially to occur in the upper part of the tidal area. Is also of frequent occurrence in channels.

× *Nereis virens* SARS. Found some few times on sand waddens and mixed waddens as well as in channels.

× *Nereis pelagica* L. According to THAMDRUP (1935), met with occasionally on the outer part of the wadden at Skallingen.

× *Nephtys hombergi* AUD. and EDW. Common on low-lying sand waddens and in channels with a stony or shelly bottom.

Sphaerodorum minimum (WEBSTER & BENEDICT). Found a single time on the sand wadden north of Fanø and on a soft wadden near Nordby (Fanø).

Goniada norvegica ØRSTED. Taken a single time off the harbour of Esbjerg.

× *Scoloplos armiger* O. F. MÜLLER. Common all over the Waddensea on sand waddens, especially their outer parts. Also frequent in shallow water in channels with a sandy bottom. Rare on waddens with a soft or a mixed bottom.

× *Pygospio elegans* CLAP. Frequent on waddens of all types, but most plentiful on sand waddens and mixed waddens. As shown by MORTENSEN (1922) and THAMDRUP (1935), it is chiefly found near the high-water mark; it may, however, also occur with frequency maxima in other places, as was the case at Skallingen in 1942 (SMIDT 1944 B) and on the wadden north of Fano in 1947 (see next chapter). May be found in small numbers in shallow water in channels.

× *Polydora ligni* WEBSTER. Eighteen individuals from six different samples were collected in the southern Danish Waddensea, and were determined by Mr. E. RASMUSSEN to be typical of this species. The species was found on all types of waddens, but predominantly on soft and mixed bottom, as well as in a channel in Ho Bay. In Königshafen near Sylt (in immediate proximity of the Danish Waddensea) WOHLBERG (1937) in the clayey bottom of a channel found, in shallow water, a very dense population (ca. 40,000 per m²) of *P. ligni*, which is stated to be taken here for the first time in "the German Bay" (southeastern North Sea). It may therefore be taken for granted that dense populations are to be found in similar localities in the Danish Waddensea. From the southern German Waddensea (in Jadebusen) LINKE (1939) reports that *P. ciliata* JOHNST. are found in dense stocks (up to 200,000 per m²) in wadden localities with a clayey bottom, especially in shallow-watered channels (Priele) in the waddens, that is to say, in quite corresponding localities to those in which *P. ligni* were found by WOHLBERG (l. c.). Further HOFKER (1930) states that *P. ciliata* is found in the Zuider Zee, exclusively burrowing in clay and peat, not, as in other places, boring in calcareous shells. HAGMEIER & KÄNDLER (1927) report the finding of *P. ciliata* boring in *Mytilus* shells at Sylt. The question now arises whether they are not identical stocks which have in some cases been identified as *P. ciliata* and in other cases as *P. ligni*. As it was shown in the present investigation (see next chapter) that very large numbers of larvae which seem to be identical with *P. ciliata* are found in the plankton, although the stocks living on the bottom are *P. ligni*, it may be doubted whether we are actually concerned with different species. Possibly they are only varieties within the same species; however, as to this point we must await thorough systematic investigations.

× *Scolecoplepis squamata* (ABILDG.). This species, which according to MORTENSEN (1922) is very numerous along the west coast of Fano, was found by THAMDRUP (1935) in small numbers on the extreme outer part of the wadden east of Skallingen.

Magelona papillicornis O. F. MÜLLER. A few individuals were taken on the outermost part of the sand wadden north of Fanø in June 1946.

Cirratulus cirratus (O. F. MÜLLER). Taken a few times in few specimens in a channel (outer part of Ho Bay, August 1942), on the outermost part of the sand wadden north of Fanø, and on the soft wadden at Nordby (Fanø).

Ophelia limacina (RATHKE). Some specimens were taken in August 1942 in the channel off the harbour of Esbjerg and in Graadyb.

× *Heteromastus filiformis* (CLAP.). Common on all types of waddens, but especially on

soft and mixed bottom, where it may be found in great abundance. Of scattered occurrence in shallow-watered channels.

Capitella capitata (FABRICIUS). Of same distribution as the preceding species, but less numerous.

× *Arenicola marina* L. Commonly distributed in the Waddensea on sand waddens and mixed waddens, but is exceedingly sparse on soft waddens. Occurs, in addition, in shallow-watered channels with sandy bottom. The adult animals are mainly found on the lower-lying parts of the waddens, while the young are most numerous near the high-water mark.

Sabellaria spinulosa LEUCK. A few lumps of sand tubes were taken in Rømø deep (August 1941) and in Graadyb (August 1942). HAGMEIER and KÄNDLER (1927) have shown that *Sabellaria* forms reefs of its sand tubes at depths between ca. 8 m and ca. 18 m, and fishermen at Esbjerg report that large blocks of *Sabellaria* tubes are found in Graadyb. Hence it may be taken for granted that it plays a great part on the hard bottom of the deeps. The large numbers of *Sabellaria* larvae, which are sometimes carried with the rising tide into the inner part of the Waddensea, lend support to this assumption.

Pectinaria koreni MALMGREN. Commonly distributed in channels, but not numerous. A few juvenile individuals were found on the outer portion of the sand wadden east of Skallingen in 1942.

× *Lanice conchilega* (PALLAS). A few individuals were taken on the sand wadden at Skallingen (THAMDRUP 1935, SMIDT 1942 B). Fragments of tubes were taken in several places in channels. Probably rather common within the area, but owing to the very deep-going tubes in which it lives it avoids capture.

Pomatoceros triqueter L. Common on stones and shells in channels.

Bryozoa:

Membranipora reticulum (L.). Common everywhere on stones and shells in channels and on waddens.

Membranipora crustulenta (PALL.). Found on shells in Ho Bay.

× *Membranipora hastingi* MARC. According to MARCUS (1940), it has been found on the Mano Flat and at Skallingen.

Alcyonidium gelatinosum (L.). A single individual was taken on *Fucus* in a channel east of Rømø in August 1941.

Gastropoda:

× *Hydrobia ulvae* PENN. Distributed on all types of waddens, where the adults are mainly found near the high-water mark, while during the summer months the young are numerous over the greater part of the waddens. Is, as a rule, sparse in the channels, but in a single case (southeast of Rømø, September 1945) it was taken in enormous quantities.

× *Littorina littorea* L. Numerous on all types of waddens, but sparse in the channels.

Buccinum undatum L. Commonly distributed nearly everywhere in channels, still it does not occur in the interior of Ho Bay.

Retusa obtusa MONTAGU. Of scattered occurrence on sand waddens. A single specimen was taken in a channel (Ho Bay).

Lamellibranchia:

× *Cardium edule* L. The adult individuals occur principally on sand and mixed waddens, where in some years they may be found in very large numbers. On soft bottom they

seem to be more sparsely present. In channels with shallow water and with sandy or mixed bottom they may likewise be present in considerable quantities. In the summer months newly settled specimens may be found in large quantities on all kinds of bottom.

× *Macoma baltica* L. Distributed on all types of waddens; in addition, in shallow-watered channels with a suitable bottom.

Tellina tenuis DA COSTA. A few individuals taken on sandy bottom in Rømø Deep. It is a surf form, which is found in large quantities on the west coasts of the islands, and which cannot be expected to occur in the inner parts of the Waddensea.

× *Scrobicularia plana* L. Found on several waddens with soft or mixed bottom (e. g. the soft wadden at Nordby). However, it is not found on sand waddens and has not been taken in channels.

× *Mya arenaria* L. Adult individuals occur commonly in patches on all types of waddens, while the newly settled young are especially abundant all over the waddens in the summer months. In addition the species occurs in channels with shallow water and a suitable bottom.

× *Mytilus edulis* L. Of scattered occurrence on waddens of all types and in channels. In several places the species forms banks exceedingly rich in individuals on the outer parts of the waddens and in channels just below the low-water mark.

× *Petricola pholadiformis* (LAMARCK). A few specimens were taken at Skallingen on a wadden with a mixed bottom (THAMDRUP 1935). Further taken on a wadden with a mixed bottom at the Rømø dam and in a channel between the southernmost point of Fanø and the mainland in the summer of 1941.

Placophora:

Chiton albus L. A single specimen was taken on the shell of a *Littorina* on the sand wadden northeast of Fanø (18/4 1946).

Crustacea:

× *Balanus improvisus* DARWIN and *Balanus balanoides* (L.). These species are abundant everywhere on waddens and in shallow-watered channels where there are possibilities for attachment (especially on *Mytilus* shells).

Jaera albifrons (LEACH.). A single individual was taken on the sand wadden north of Fanø.

Idothea baltica (PALLAS) and *Idothea viridis* (SLABBER) are of scattered occurrence on sand waddens and waddens with a mixed bottom.

× *Bathyporeia pilosa* LINDSTR. = *B. robertsoni* BATE (see WATKIN 1938). Occurs in most places on sand waddens and in channels with sandy bottom. That it is chiefly a sandy-bottom and surf animal, is shown by its very numerous occurrence at the seashore along the west coasts of the islands.

Bathyporeia (elegans WATKIN?). Found at a single station between Fanø and the mainland.

Gammarus zaddachi SEXTON. Scattered on waddens (pools) and in channels.

× *Corophium volutator* (PALLAS). Occurs on waddens of all types, but only in large numbers on waddens with a soft or a mixed bottom and on sand waddens nearest the shore. Found, also, in shallow water in channels with a soft or a mixed bottom. Its quantitative occurrence is subject to very great fluctuations.

Caprella linearis (L.). A single specimen taken on a sand wadden at the small island of Jordsand south of Rømo.

× *Mysis flexuosa* O. F. MÜLLER. Numerous in channels, where it may be taken in considerable quantities with the young-plaice trawl. In addition it occurs occasionally in pools on the waddens at low-water.

Cumopsis goodsiri v. BENEDEN. A few specimens were taken on sand waddens north and northeast of Fanø. A single specimen was taken in the channel off the harbour of Esbjerg, whirled up into the water.

Lamprops fasciata G. O. SARS. A single specimen taken in the channel off the harbour at Esbjerg.

× *Crangon vulgaris* FABR. Very numerous in the channels, where it is caught in large quantities with the young plaice trawl. At flood-tide it migrates in over the waddens, and a few may be found here at low-water, buried in the bottom. The young are very frequently found on the waddens in summer.

Eupagurus bernhardus L. Common in channels throughout the Waddensea except in the interior of Ho Bay, as it ceases to occur even off Hjerting. A few individuals are occasionally met with on the waddens.

× *Carcinus maenas* L. Abundant everywhere in the channels, where it may be taken in large quantities with the young plaice trawl. Adult individuals are only occasionally met with on the waddens, while the young are common here in the summer months.

Portunus holsatus FABR. Taken now and then in channels.

Echinodermata:

Asterias rubens L. Common everywhere in the channels except in the interior of Ho Bay. Abundant off Hjerting, and young individuals were found northward as far as Sælborg.

Psammechinus miliaris (GMELIN). Found in most places in channels, but hardly in great numbers. Not taken in the interior of Ho Bay.

Tunicata:

Botryllus schlosseri PALLAS. Taken in the harbour at Esbjerg on the under side of a jolly-boat.

Molgula sp. Taken in the same place as the preceding species.

C. Discussion.

In the following pages questions concerning the occurrence of the bottom animals and the factors forming their environment are discussed.

While on the waddens living species are capable of enduring the very great variations of temperature, salinity, and water-covering, etc., to which they are constantly exposed, the species that are especially associated with the channels must be assumed to be far more sensitive to one or several of these factors. Thus, in agreement with this it is seen that while almost all the species living on the waddens are also met with in the channels, a considerable number of the species that live in the channels are never or quite exceptionally met with on the waddens. Some typical examples of channel animals which do not tolerate low salinities are *Asterias rubens*, *Psammechinus miliaris*, *Eupagurus bernhardus*, and *Buccinum undatum*, as these species are not found in the inner part of Ho Bugt, but seem to disappear off, or some distance north

of, Hjerting (occasional young individuals of *Asterias* have been met with as far towards the interior of the bay as off Sælborg). In accordance with this is the distribution of these species towards the Baltic, none of them, with the exception of *Asterias* (which has been found even quite close to the Pommeranian coast), occurring beyond the threshold Gedser—Darsør Ort. No doubt we are here concerned with an osmoregulatory ability.

As it is the animal life of the waddens that is of the greatest interest in the present paper, these will be treated at some length; thus 1) an account will be given of the different faunal zones on the waddens, 2) the distribution of some of the most important species in relation to the biotope will be explained, and finally 3) the effect of some of the environmental factors will be discussed.

1) Faunal zones on the waddens:

In his study of the fauna on the sand wadden north of Fanø, WESENBERG-LUND (1904) distinguished between a zone nearest the land, which he called the *Corophium* belt, and, outside this, a zone called the *Arenicola* belt. MORTENSEN (1922) calls these two zones in the same wadden area the *Corophium-Pygospio*-belt and the *Arenicola-Cardium*-belt. An entirely corresponding zonation was ascertained by THAMDRUP (1935) on the sand wadden east of Skallingen, since nearest land there was a belt with the character animals *Corophium volutator*, *Pygospio elegans*, and *Hydrobia ulvae*, while the outer belt was characterised by *Arenicola marina*, *Cardium edule*, and *Macoma baltica*.

During my investigations on the sand wadden north of Fanø, I found in the main the same two zones, to which, however, I will add some comments: *Corophium volutator* mostly occurs with a maximum nearest the shore, but is subject to very great fluctuations from year to year and in the course of the year. *Pygospio elegans* has, as a rule, its maximum occurrence nearest the shore, but deviations from this rule may occur, as in 1947, when it was present in very considerable numbers on the extreme outer part of the sand wadden, where a low flattened sand ridge had formed at the point where the wadden sloped down towards the channel. Adult *Hydrobia ulvae* have a maximum nearest the shore, but in summer the 0-group is found in large quantities all over the wadden, especially its outer part. Adult *Arenicola marina* and *Cardium edule* mainly occur in the outer zone, while young *Arenicola* have their maximum in the inner zone. *Macoma baltica* in small numbers are scattered over the greater part of the wadden. It should be added that *Nereis diversicolor* is most frequent in the inner zone, while *Scoloplos armiger* and *Nephtys hombergi* predominantly occur in the outer zone; (THAMDRUP (1935), at Skallingen, found varying maxima for *Nereis diversicolor*, a maximum for *Scoloplos armiger* some distance towards the interior of the wadden, and a maximum for *Nephtys hombergi* on the outer part of the wadden).

The collections made in 1941 in the southern and middle parts of the Danish Waddensea likewise show that the zonation demonstrated by THAMDRUP (l. c.) holds good in all essentials for rather evenly sloping sand waddens. If, however, the waddens present highly varying levels and varying composition of the bottom material, conditions will be far more complicated.

In the German Waddensea WOHLBERG (1937) and LINKE (1939) have investigated the composition of the wadden fauna in relation to the conditions of the bottom. WOHLBERG (l. c.) demonstrated various sediment areas with associated character animals in Königshafen at Sylt. It is of special interest that on the typical sand wadden he found two different zones, corresponding to those found at Skallingen and on the wadden north of Fanø, viz. a) an upper zone characterised by young of *Arenicola marina*, *Clitellio arenarius*, and *Pygospio elegans*, and

b) a lower zone with older individuals of *Arenicola marina*, *Scoloplos armiger*, *Nephtys hombergi*, *Cardium edule*, and *Tellina tenuis*.

In his work from Jadebusen, LINKE (l. c.) divides the *Macoma baltica* community living on the waddens into eight different variations, which harmonise well with the aforementioned zonal division. The following four variations are of the greatest interest in this discussion: 1) the *Corophium* variation (dominant species: *Nereis diversicolor*, *Pygospio elegans*, *Heteromastus filiformis*, *Pelosclex benedeni*, *Corophium volutator*; — bottom: varying from sandy to soft bottom, but always sheltered against disturbances due to the movements of the water; — occurrence: by far the greater part near the land). 2) The *Scrobicularia* variation (dominant species: *Scrobicularia plana*, *Mya arenaria*, *Hydrobia ulvae*, *Nereis diversicolor*; — bottom: soft bottom, only disturbed when the sea is very high; — occurrence: several places as a zone outside the *Corophium* variation). — 3) The *Pygospio* variation (dominant species: *Cardium edule*, *Pygospio elegans*, *Arenicola marina*; — bottom: mixed bottom, re-deposited only when the sea is rather high; — occurrence: a fairly broad zone outside the zones mentioned above). — 4) The *Scoloplos* variation (dominant species: *Nephtys hombergi*, *Scoloplos armiger*, *Arenicola marina*, *Bathyporeia (robertsoni)*, *Tanaissus lilljeborgi*; — bottom: sandy bottom, which is constantly re-deposited; — occurrence: a broad outer wadden-zone).

All the above-mentioned investigations of zones within the wadden fauna show in the main good agreement; but they also show some rather complicated conditions, resulting from the interaction of several factors. These conditions will be discussed under 2) and 3) below, and in this discussion, besides of the said investigations, mention will be made of two interesting investigations in British estuaries (SPOONER and MOORE 1940, BEANLAND 1940).

2) Distribution of species in relation to biotopes:

On the basis of the available investigations it will be briefly shown how the distribution of some of the most important species are determined by the different factors. These questions have especially been treated by THAMDRUP (1935).

Nereis diversicolor.—Investigations carried out by THAMDRUP (1935), WOHLBERG (1937), LINKE (1939), BEANLAND (1940), SPOONER and MOORE (1940) and my own investigations agree in showing that the species tolerates very different conditions of life, being found nearly all over the waddens. It seems, however, to show a certain preference for the upper part of the tidal zone and for a soft bottom. Hence it is possible, as assumed by SPOONER and MOORE (l. c.), that it thrives best where the bottom is sheltered against too heavy movements of the water.

Nephtys hombergi.—The available investigations (THAMDRUP 1935, WOHLBERG 1937, LINKE 1939, SPOONER and MOORE 1940, and the present investigation) show that the species occurs quite predominantly on low-lying sand waddens and in shallow-watered channels with a sandy bottom. Accordingly the character of the bottom seems to be of importance; and moreover it is assumed (according to THAMDRUP, l. c.) that the duration of the water-covering is of decisive influence.

Scoloplos armiger.—Available investigations (THAMDRUP 1935, WOHLBERG 1937, LINKE 1939, SPOONER and MOORE 1940, BEANLAND 1940, SMIDT 1944 B, and the present investigation) show that the species prefers sandy bottom and that it is especially found in the middle and outermost wadden areas. Since, like *Arenicola*, it is a bottom-feeder, it is probable that its distribution towards the inner parts of the wadden is limited by its requirement of no too considerable moisture of the bottom material (according to THAMDRUP, l. c.).

Pygospio elegans.—Available data (THAMDRUP 1935, WOHLBERG 1937, LINKE 1939, BEANLAND 1940, and the present investigation) show that the species occurs on various kinds of bottom, though with preference on sandy and mixed bottom. In general it is most numerous on high-lying wadden areas (especially near land), but this is no indispensable rule. Possibly its distribution is to some extent determined by competition for space on the part of *Cardium* (THAMDRUP, l. c.). At the beginning of the 1930's, when an abundant stock of *Cardium* was found on the wadden at Skallingen, *Pygospio* had been forced right up towards the high-water mark, but in 1942, when the *Cardium* stock had been destroyed, *Pygospio* had spread across the wadden (SMIDT 1944 B).

Heteromastus filiformis.—Investigations by WOHLBERG (1937) and LINKE (1939) as well as the present investigation show that the species prefers a soft or a mixed bottom.

Arenicola marina.—Investigations of the distribution within tidal areas (WESERBERG-LUND 1904, MORTENSEN 1922, THAMDRUP 1935, WOHLBERG 1937, LINKE 1939, BEANLAND 1940, SMIDT 1944 B, NEWELL 1948, CHAPMAN and NEWELL 1949, and the present investigation) show that the adult animals are predominantly found on the outer portions of the waddens, avoiding the higher-lying areas. WOHLBERG (l. c.) and the present author noticed that it is especially concentrated in depressions in the waddens. Moreover all the papers mentioned show that *Arenicola* is most frequent on sandy bottom, but decreases rapidly in number with increasing softness of the bottom, being exceedingly sparsely present on a markedly soft bottom; according to CHAPMAN and NEWELL (1949), the species is chiefly found in sandy bottom mixed with mud. Unlike the adult animals, the quite young individuals mainly occur on the inner portions of the waddens nearest the shore (THAMDRUP l. c., WOHLBERG l. c., NEWELL l. c., next chapter of the present paper). Conclusion: Two factors seem to determine the distribution of the adult individuals of *Arenicola*. In the first place, the character of the bottom, the species showing a marked preference for sandy bottom. Secondly, the degree of moisture of the bottom (THAMDRUP 1935), since, to be able to feed, the species requires a thoroughly moist bottom, and it is in accordance with this that it is especially concentrated in depressions.

Hydrobia ulvae.—Most investigations show that the species is independent of the quality of the bottom, but that its occurrence is most concentrated in the upper part of the tidal area (THAMDRUP 1935, WOHLBERG 1937, LINKE 1939, SPOONER and MOORE 1940, BEANLAND 1940). The author's own investigations on the wadden north of Fanø showed that this concentrated occurrence on the uppermost portion of the wadden only applies to the adults. The young are found scattered all over the wadden in large quantities in summer and autumn (see next chapter), where the greater part of them are consumed, while the remainder seek towards the shore. As *Hydrobia* lives on and in the extreme upper layer of the bottom, it is possible that its preference for the inner wadden zone is due to the disturbing influence of the water movement on this bottom layer on the middle and outer parts of the wadden.

Cardium edule.—A consideration of the various investigations of the occurrence of the species (MORTENSEN 1922, THAMDRUP 1935, WOHLBERG 1937, LINKE 1939, SPOONER and MOORE 1940, BEANLAND 1940, and the present investigation) will show that it is rather independent of the bottom material, but that it is not found in the uppermost portion of the wadden near the high-water mark. Much speaks in favour of the view put forward by THAMDRUP (l. c.) that its occurrence is determined by the fact that, being a suspension feeder, it requires a water-covering period of no too short duration.

Macoma baltica.—Available data (THAMDRUP 1935, WOHLBERG 1937, LINKE 1939, SPOONER and MOORE 1940, BEANLAND 1940, and the present investigation) show that the

species is independent of the bottom material, being of scattered occurrence on all types of waddens. THAMDRUP (l. c.) thinks that it is capable of securing sufficient food if only the wadden is covered with a quite thin water layer (e. g. in shallow pools), since with its siphon it sucks up the water from the surrounding bottom.

Mya arenaria.—According to the available information (THAMDRUP 1935, LINKE 1939, and the present investigation), the species seems to be independent of the bottom material. According to THAMDRUP (l. c.), its distribution is possibly restricted by the duration of the period of water-covering in the same way as that of *Cardium*.

Scrobicularia plana.—All the available data (THAMDRUP 1935, WOHLBERG 1937, LINKE 1939, SPOONER and MOORE 1940, BEANLAND 1940, and the present investigation) show that the species has a marked preference for a soft bottom, and that it is confined to soft and mixed bottoms. Thus it seems to be the character of the bottom which is the decisive factor for its distribution.

Mytilus edulis.—The available information (HAGMEIER and KÄNDLER 1927, THAMDRUP 1935, LINKE 1939, and the present investigation) show that *Mytilus* chiefly occurs on low-lying areas, especially near and below the low-water mark. The most probable explanation is that put forward by THAMDRUP (l. c.), viz. that the duration of the period of water-covering is the decisive factor for the distribution, *Mytilus*, like *Cardium* and *Mya*, being a suspension feeder.

Corophium volutator.—The species is found on the sand wadden east of Skallingen with a marked maximum nearest the high-water mark (THAMDRUP 1935, SMIDT 1944 B). The same is the case on the sand wadden north of Fanø, as demonstrated by WESENBERG-LUND (1904), MORTENSEN (1922), and the present investigation. It was shown by my investigations to be the case in other places, also, in the Danish Waddensea; further it was found that the species is especially frequent on soft bottom both in wadden areas and in channels (inner Ho Bay). In the German Waddensea WOHLBERG (1937) found that in Königshafen (Sylt) it occurred in a belt a little below the high-water mark both on sandy and muddy bottoms. LINKE (1939), in Jadebusen, showed that it is found on the inner part of the wadden on sandy as well as on soft bottom not exposed to re-deposition. In England, SPOONER and MOORE (1940) and BEANLAND (1940) showed that in estuaries it attains its maximum occurrence near the high-water mark, where it is sheltered against too violent water movements. BEANLAND (l. c.) is of opinion that it sometimes swims about, to settle where the water is calm. Conclusion: All these data support the view that the factor which limits the occurrence of the species is a too violent water movement, for everywhere the species seems to prefer such localities as are sufficiently sheltered to prevent a constant re-deposition of the bottom material. The composition of the bottom material, however, seems to be of subordinate importance. The theory propounded by THAMDRUP (l. c.), that it is competition for space on the part of *Cardium edule* which prevents *Corophium* in spreading over the wadden, appears to me, according to the above statements, little probable, notably because it has turned out (SMIDT 1944 B) that the species did not, as might be expected, spread over the wadden at Skallingen in 1942, when the *Cardium* stock had been destroyed after the severe winters, but still remained concentrated near the high-water mark.

3) Effects of the environmental factors:

As the various factors were treated in fairly great detail by THAMDRUP (1935), they will be mentioned more summarily here:

The quality of the bottom has a more or less limiting influence on a number of

species (*Scrobicularia plana*, *Pygospio elegans*, *Heteromastus filiformis*, *Arenicola marina*, *Scoloplos armiger*, *Nephtys hombergi*). Other species (*Corophium volutator*, *Hydrobia ulvae*, *Nereis diversicolor*, *Cardium edule*, *Macoma baltica*, *Mya arenaria*) seem almost to be indifferent to this factor.

The period of submersion must be regarded as a limiting factor for the suspension feeders (*Cardium edule*, *Mya arenaria*, *Mytilus edulis*). Further, it seems to be of importance for *Nephtys hombergi*.

The moisture of the soil must be assumed to be of importance for the bottom feeders (*Arenicola marina*, *Scoloplos armiger*, *Heteromastus filiformis*). Species like *Macoma baltica* and *Scrobicularia plana*, which suck out the surrounding bottom with their siphons, require so much moisture that the wadden is covered by a thin water layer.

The motion of the water was not treated by THAMDRUP (l. c.); however, great importance is attached to it by SPOONER and MOORE (1940), and BEANLAND (1940), who are of opinion that violent movements of the water, which will constantly bring about a re-deposition of the upper bottom layers, limit the distribution of certain species (thus within the area under consideration *Corophium volutator*, *Hydrobia ulvae*, and *Scrobicularia plana*?). Other species, on the other hand, seem to prefer strong movements of the water, for they are found in abundance along the west coasts of the islands, but are only sparsely present in the Waddensea (*Scolecoplepis squamata*, *Bathyporeia pilosa*, *Tellina tenuis*).

In extreme cases the temperature (especially frost periods of long duration) exerts a considerable influence on the bottom fauna, especially on species living at the surface of the wadden (THAMDRUP 1935, SMIDT 1944 B, the present paper chapters VII and XI).

The salinity, like the temperature, probably has an appreciable influence in extreme cases; but to all the wadden species it applies that they are capable of tolerating very considerable variations in the salinity. It will be of interest, however, to mention here that SPOONER & MOORE (1940) on investigating a British estuarial fauna, erected three groups of species on the basis of their dependence on the salinity: Group A, primarily marine species (i. a. *Phyllodoce maculata*, *Scoloplos armiger*, *Lanice conchilega*, *Carcinus maenas*, *Littorina littorea*, *Cardium edule*); group B, marine and estuarial species (*Nephtys hombergi*, *Macoma baltica*); group C, more or less strictly estuarine species (*Hydrobia ulvae*, *Corophium volutator*, *Scrobicularia plana*, *Nereis diversicolor*).

The quantity of nutritive substances no doubt plays a part in connection with, and partially determined by, other factors (the water-covering period, moisture condition of the bottom, temperature).

Biological competition.—THAMDRUP (l. c.) is of opinion that the competition for space between *Cardium edule* and *Corophium volutator* is the chief factor limiting *Corophium* to the inner tidal zone. However, there is not much of what has been stated above that supports this view, whereas such a relation possibly exists between *Pygospio elegans* and *Cardium edule*.

Finally it should be pointed out that since a cooperation of factors will always be active in nature, it will be difficult and often impossible to decide which factor is the decisive one, and hence much of what has been said above has acquired so hypothetical a character.

VII. Life-histories of the most important Species of the Macrofauna of the Bottom.

This chapter is closely connected with the next one, in which the occurrence of the pelagic bottom animal larvae is treated, and the summary and discussion given in the succeeding chapter is of essential importance as a continuation of the summary and discussion in this chapter. The species treated here are such as are of significance for the animal production and have been made the subject of observation.

POLYCHAETA.

A. Special part:

Phyllodoce maculata ØRSTED.

The gelatinous egg-masses (fig. 15A) are of common occurrence on the waddens in April and May, where they are safely anchored to the bottom with long branched prolongations. They correspond closely to those described by MCINTOSH (1869) and NORDGAARD (1912), and are easily recognisable by their content of green eggs, which are present in numbers of at least 10,000 per egg-mass. All the eggs in the egg-masses observed were at the same stage of develop-

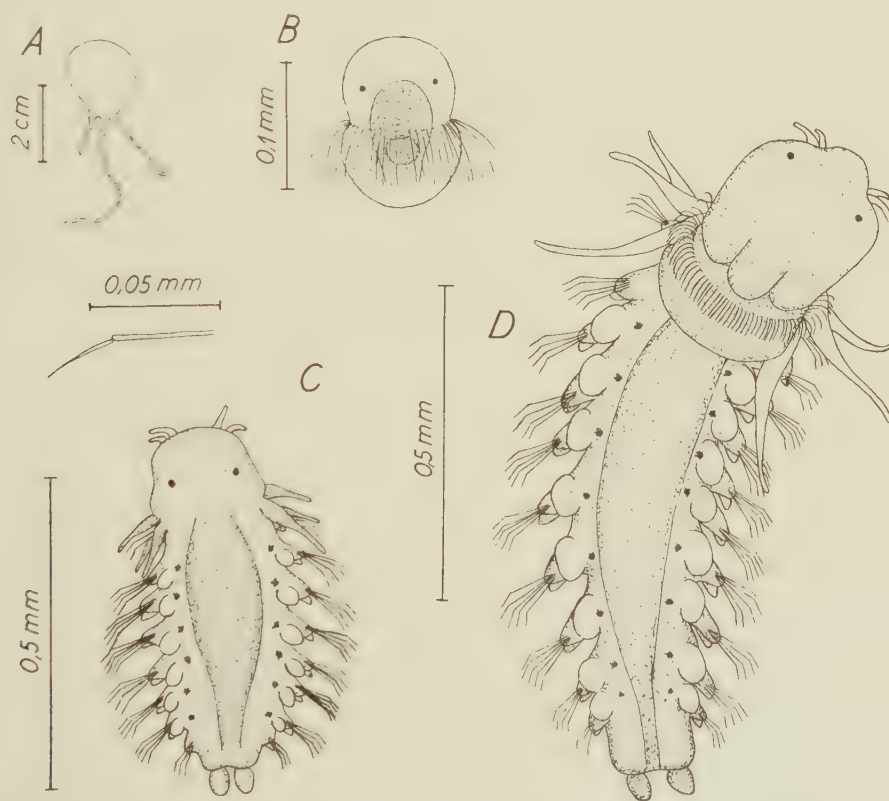


Fig. 15. *Phyllodoce maculata*. A. Egg-mass (sand wadden north of Fanø $21/3$ 1946). — B. *Trochophora* (observed swimming out of an egg-mass $20/5$ 1946). — C. *Nectochaeta* (high-water sample from Esbjerg Havneløb $20/6$ 1943, drawn from preserved sample). — D. *Nectochaeta* (high-water sample taken off Esbjerg $9/6$ 1942; drawn from preserved sample).

ment. From egg-masses transferred to glass vessels a large number of small *Trochophora* (fig. 15 B) swarmed out into the water. They were recognisable by their green intestine, and moreover they were provided with a pair of red eye spots, a prototroch, and an oral orifice. These *Trochophorae* may at times be found in large numbers in the plankton.

In the summer months and till well into the autumn a few *Nectochaeta* may occasionally be met with in the plankton, in most cases in high-water samples. They agree well with the larva described by THORSON (1946) and are easily recognisable by two rows of dark pigment spots along the dorsal side. Those figured here (fig. 15 C + D) were drawn from preserved material, in which the pigment had paled somewhat.

Observations on the growth of the bottom stages are not available. The density of adult individuals is comparatively slight, there being mostly less than 50 per m² and very rarely more than 100 per m².

***Eteone longa* FABR.**

Spawning not observed in the Waddensea. According to MEEK and STORROW (1924), it takes place while the parent animals swim freely about in the water, when a large number of eggs are emitted without the formation of egg capsules. A few larvae agreeing with those

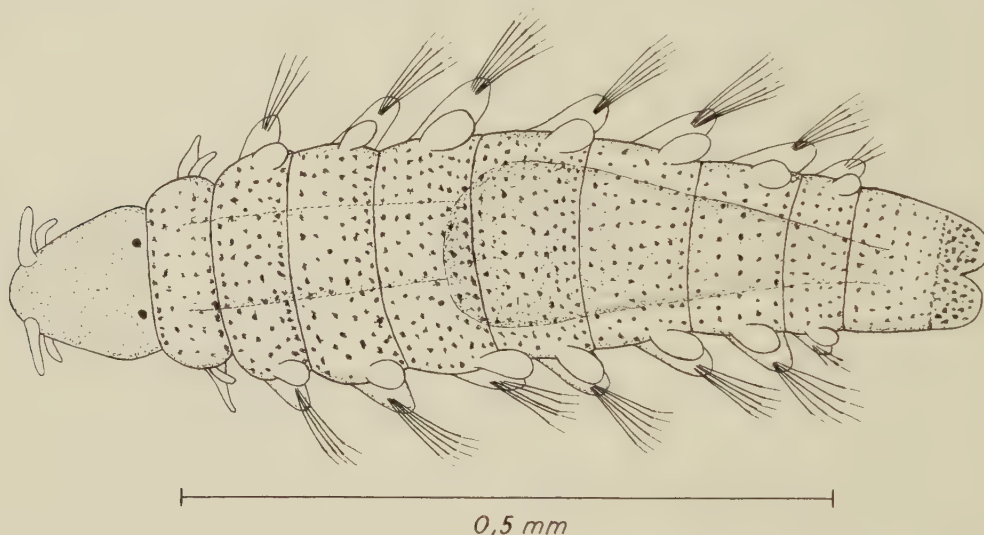


Fig. 16. *Eteone longa*, newly settled stage (sand wadden north of Fano ¹⁵/₅ 1942; drawn from preserved sample).

described and figured by THORSON (1946) have now and then been observed in the plankton (in high-water plankton on ¹⁵/₅ 1942, ²⁹/₈ 1943, ¹/₈ 1944, and ¹⁹/₈ 1944. In addition a large larva was taken in a micro bottom sample on the sand wadden at Fano on ¹⁵/₅ 1942 (fig. 16). No further information about the reproduction and growth of the species is available.

The adult individuals, somewhat more abundant than *Phyllodoce maculata*, are rarely found in greater numbers than 100 per m².

***Nereis diversicolor* O. F. MÜLLER.**

1) Reproduction:—Information about the period of maturity of the species in the Waddensea is found in the literature. Thus THAMDRUP (1935) states that from the middle of

April till some time in May large numbers of mature individuals have been observed at Skallingen, and as late as July ♀♀ with mature eggs were often found. LINKE (1939) reports from Jadebusen that mature individuals of *Nereis diversicolor* are found in March–May, and in April–May many dead worms are present on the wadden; hence LINKE thinks that a number of the worms die after spawning. According to these statements it may be assumed that the main spawning by the worm population of the wadden takes place late in April or at the

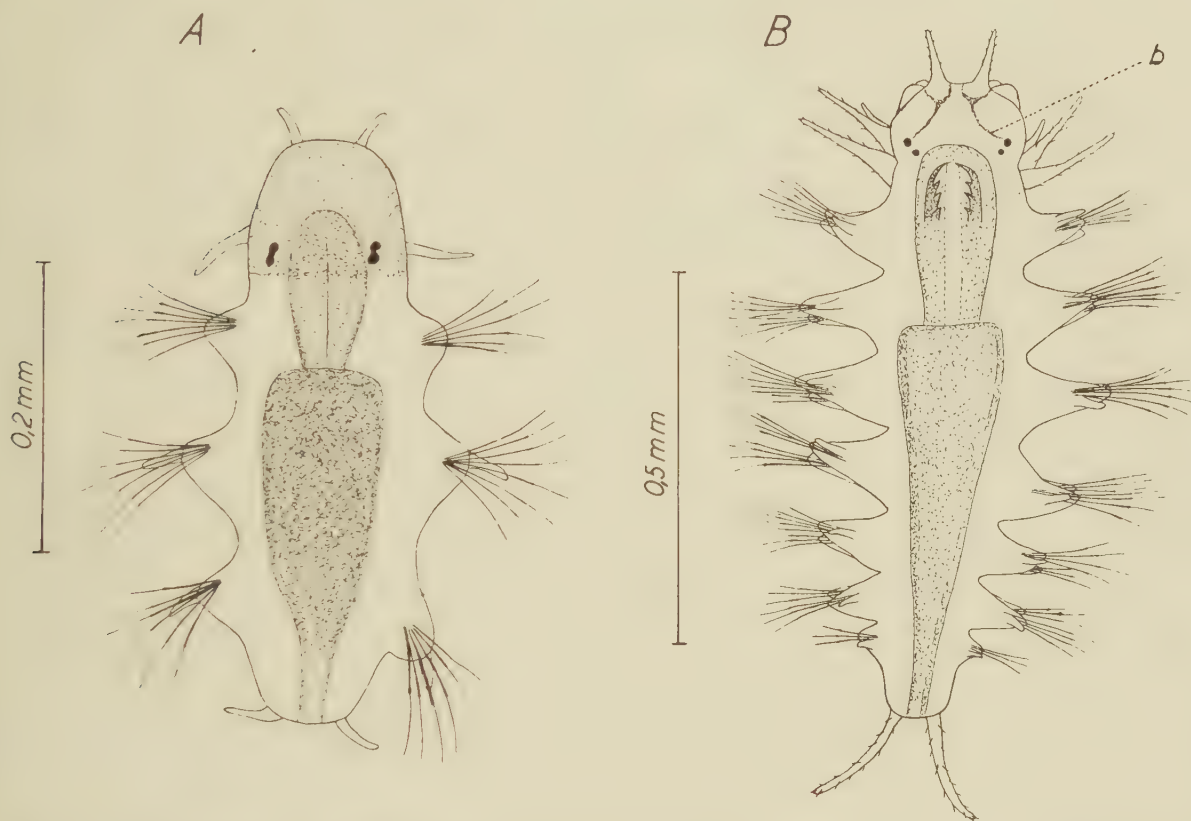


Fig. 17. *Nereis diversicolor*. A. Youngest bottom stage, from sand wadden north of Fanø $15/6$ 1949 (drawn from preserved specimen, eyes carmine, intestine dark). — B. Older bottom stage from the sand wadden northeast of Fanø $16/8$ 1946 (drawn from life; eyes black, b = black pigmentation on the head).

beginning of May, and that spawning may, in addition, take place till late in the summer. According to HERPIN (1925) the spawning takes place by rupture of the body wall.

A true pelagic larval stage, if any, can probably only be of short duration, as such a stage was not observed in the plankton samples; but quite young individuals with down to three chaetigerous segments (fig. 17), which in May may be found in large numbers on the wadden, are often whirled up in the water, and accordingly they are often found in plankton samples. In 1947, which seemed to be a rich breeding year for the stock, considerable numbers of these larvae were found in plankton samples taken on May 22 (in the high-water sample 40 per m^3 , in the low-water sample 22 per m^3 of water) and July 23 (in the high-water sample 22 per m^3 , in the low-water sample none). These larvae are capable of making lively swimming

movements by sideways undulations of the body, and they have been found in plankton samples with up to seven chaetigerous segments. They have been found during the whole summer and autumn till some time in December, and since in most cases they were taken in high-water plankton, there is reason to assume that they have chiefly been carried in from areas farther out. The young individuals described above correspond to the youngest bottom stages described by McINTOSH (1907) from St. Andrews (Scotland), which, like those found in the Waddensea, had as few as three chaetigerous segments. Furthermore the stages from the Waddensea entirely resemble the stage II described and figured by the author (SMIDT 1944 A) from the harbour of Copenhagen, the head exhibiting the same black pigment pattern. On the other hand, the lecithotrophic larval type, which has been described and figured by the author (SMIDT l. c., fig. 5 I) from the harbour of Copenhagen and by THORSON (1946) from the Sound, has not been observed in the Waddensea. In a recently published and very thorough work by R. PHILLIPS DALES (1950) some larval stages are described and figured which much resemble those of the Waddensea, but differ from them by lacking the black pigment in the head region. In agreement with the reports from the Waddensea, DALES states that the larvae develop in the mud and that there is no true pelagic phase.

2) Growth.—Studies of the growth of the progeny were made on the sand wadden north of Fano in 1946 and 1947. The material was collected with a skimmer (younger stages) and with a $1/100$ m² core sampler (older stages). The smallest bottom stages observed were taken on the outer wadden in large numbers on $^{26}_{/5}$ 1947; they had 3–7 chaetigerous segments and a mean length of 0.8 mm. From this size the young in the course of the summer and autumn grow to an average size of about 2 cm, varying somewhat from year to year. The results of the measurements made in the aforementioned two years are shown diagrammatically in fig. 18. The curves show the average lengths during the season, and these were computed on the basis of the following material (for each date the number of measured individuals and the length in mm of the largest and the smallest individual are given): 1946: $^{18}_{/5}$

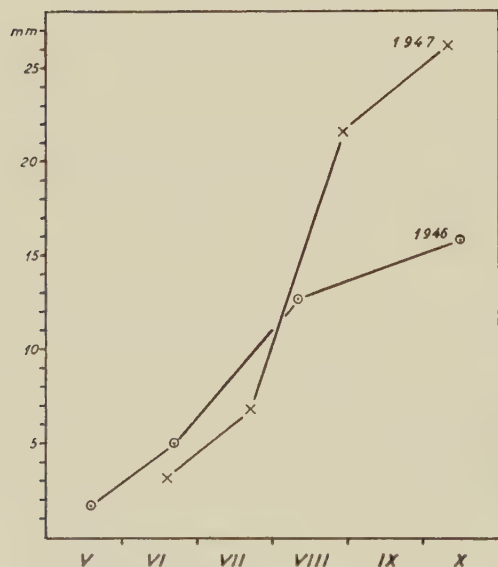


Fig. 18. Growth curves for the 0-groups in 1946 and 1947.

(26, $1\frac{1}{2}$ – $2\frac{1}{2}$ mm), $^{24}_{/6}$ – $^{26}_{/6}$ (146, 3–11 mm), $^{10}_{/8}$ (34, 5–29 mm), $^{16}_{/10}$ (71, 5–26 mm); 1947: $^{18}_{/6}$ (67, $1\frac{1}{2}$ –10 mm), $^{22}_{/7}$ (78, 3–17 mm), $^{29}_{/8}$ (23, 7–42 mm), $^{10}_{/10}$ (10, 19–38 mm). Both curves show that the highest rate of growth was found in the summer months July–August, decreasing, subsequently, in the course of the autumn. It is natural to connect the appreciably higher growth-rate in 1947 than in 1946 with the exceptionally fine weather during the summer and late summer of 1947. The rather great variation of the young at the end of the growth period is a natural consequence of the fact that fresh broods are constantly added. The greatest length measured on a 0-group *Nereis* on the wadden was 42 mm ($^{29}_{/8}$ 1947). Growth to a similar size to that in nature was observed in the laboratory; 14 larvae with 5–13 chaetigerous segments were placed in glass dishes on $^{16}_{/5}$ 1946; one of these larvae was alive and thrived well about the middle of August, when it had attained a length of ca. 3 cm.

3) Quantitative occurrence and mortality: In the preceding chapter it was stated that in most places the species was most abundant in the upper zone of the waddens, as is the case on the wadden north of Fano. The young, however, are found in great abundance over the greater part of the wadden, as in 1947, which appears to have been a year with a very prolific brood. The figures below illustrate the conditions on the wadden north of Fano that year, indicating the numbers of 0-group *Nereis* per m² distributed over the line of sampling, whose length between the low-water mark and the high-water mark is ca. 450 m.

	Distance from low-water mark	near low- water mark:	120—190 m	280—320 m	430—440 m
Date: 25/5		16,000	69,000	4,900	500—1000
18/6		(300)	23,000	12,800	1,900
21/7		—	(200)	2,000	10,000
29/8		—	(100—200)	(200)	800—900
10/10		—	(100)	?	500

These figures show that in the course of the summer the progeny as a whole had been much reduced, and that a migration had taken place from the outer part of the wadden towards the high-water mark, a colossal reduction on the outer and middle parts of the wadden having occurred simultaneously with a considerable increase in the number of young on the inner part of the wadden (the last samples disregarded). A corresponding spreading of the young with a subsequent migration towards the inner part of the wadden was, however, not observed in 1946, but it is conceivable that the reduction in the outer and middle wadden areas took place so rapidly that the young had disappeared before the sampling.

Adult *Nereis* were only found in small numbers (rarely more than 100 per m²); it is possible, however, that some of the largest worms are so deeply buried in the bottom that they avoid being taken with the samples, so the figures may be somewhat too low. In any case, however, there is undoubtedly a very high death-rate among the young, which must be ascribed to the persecution by enemies, the young *Nereis* constituting an important food element for bottom fish, carnivorous bottom invertebrates, and birds.

Nephtys hombergi AUD. & EDW.

1) Reproduction.—Spawning in the Waddensea must be assumed in the main to take place in the early summer. THAMDRUP (1935) found individuals with eggs on 17/3, but not in the numerous samples taken in July. In my investigations the largest numbers of larvae (pelagic and newly settled) were found in the period June—August, a single one even as late as October. It is probable, therefore, that the main spawning takes place in May—June.

The youngest larval stage (*Trochophora*), described by FUCHS (1911) and WILSON (1936), has not been identified in the plankton samples, whereas the succeeding *Nectochaeta* stages, not previously known, were identified. Fig. 19A shows a young *Nectochaeta* stage from a plankton sample. It is characteristic by having an intense dark pigmentation around the anus and a distinct brown pigmentation on the head. Dorsally the brown head pigment is bounded by a distinct V-shaped marking. Fig. 19B shows a later stage, in which the V-shaped marking is even more distinct. In addition there is a faint brown pigmentation dorsally on the parapodia. The distinct anal pigmentation in this stage is likewise brown, and behind it there is a faint yellow pigmentation. The intestine is green.

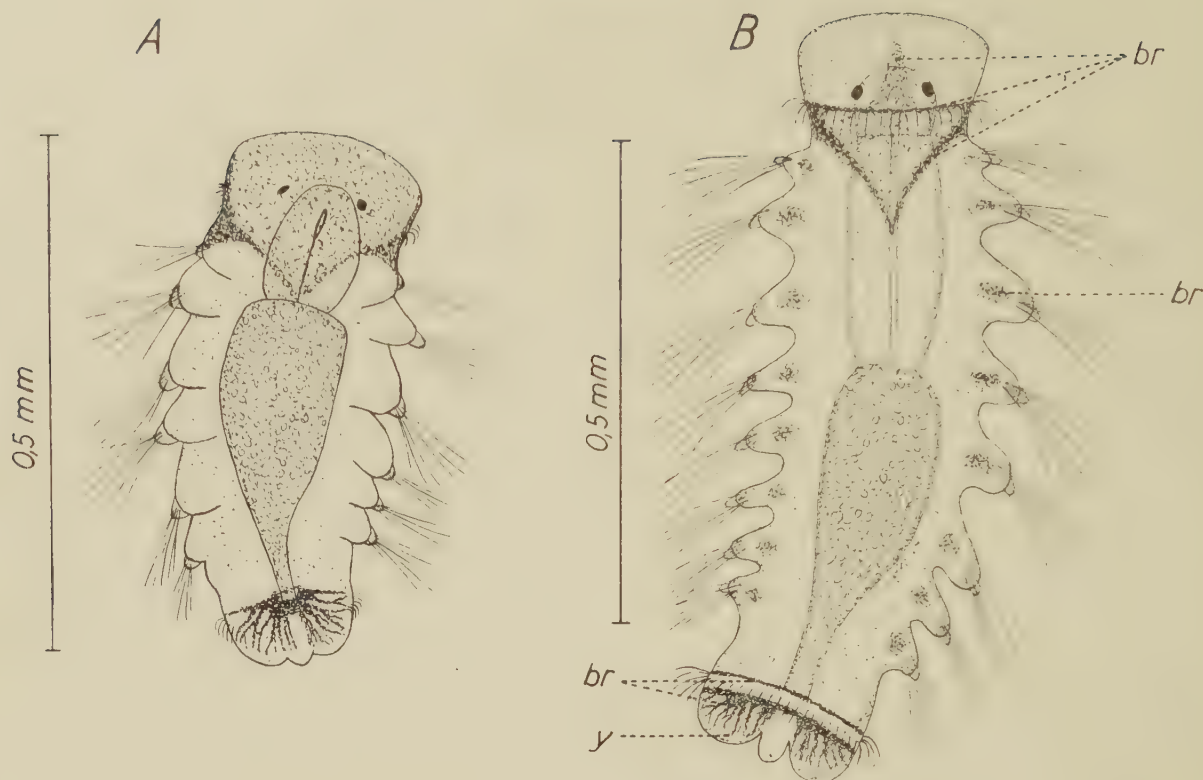


Fig. 19. *Nephtys hombergi*. A. Young *Nectochaeta* from high-water plankton at Esbjerg $^{21}/_7$ 1942 (drawn from life; eyes black, brown pigmentation on the head and around the anus). — B. Older *Nectochaeta* from high-water plankton off Esbjerg $^{29}/_8$ 1943 (drawn from life; intestine green, br = brown pigmentation, y = yellow pigmentation).

These *Nectochaeta* stages were found in plankton samples taken off Esbjerg in the months of June, July, August, and October. As they were always only taken in very few specimens, and as they resemble the youngest bottom stages found on the waddens, it must be assumed that they are not actually pelagic, but have been whirled up from the bottom.

These larvae I have without hesitation referred to the species *Nephtys hombergi*, as it is the only *Nephtys* species that has been taken in the Wadden-sea, and the larvae differ distinctly from the other *Nephtys* larvae described from Danish waters (THORSON 1946).

The growth of the young bottom stages is illustrated in fig. 20, which, however, must be accepted with some reserve, since the material measured, taken on the sand wadden north of Fanø, is very limited. The average length on $^{22}/_6$ 1946 was ca. 1.5 mm (12 individuals measured, number of chaetigerous segments 8—18), on $^{10}/_8$ ca. 11 mm (6 individuals measured,



Fig. 20. Growth curve for the 0-group in 1946.

ranging between 6 and 16 mm), and about the middle of October ca. 18 mm (9 individuals ranging between 6 and 30 mm).

2) Quantitative occurrence and mortality.—The newly settled larvae were only found in comparatively small numbers and chiefly in June—July, further, on a single occasion late in May and once about the middle of October. The largest numbers were found in June, 1946, ca. 1000 individuals per m^2 occurring on the outer part of the sand wadden north of Fanø on June 22. In the same locality 120 juveniles per m^2 were found about the middle of October of the same year, that is to say, only well over 10 per cent. of the newly settled brood, a reduction that must be ascribed to the persecution by enemies. Adult individuals were never found in numbers exceeding 100 per m^2 , and in by far the majority of cases (in material collected in 1941 in the southern Waddensea and material collected later in the northern Waddensea) the density was about 10–20 per m^2 , in some cases even less (these latter figures correspond to those found by THAMDRUP (1935) on the wadden at Skallingen).

***Scoloplos armiger* O. F. MÜLLER.**

1) Reproduction and Growth. — Spawning takes place in the Waddensea in spring. According to HAGMEIER & KÄNDLER (1927), THAMDRUP (1935), and LINKE (1939), the egg-masses are found on the waddens from February till some time in May. During my investigations they were found in March–April, but not in May. The egg-masses, which have been described and figured by several authors (cf. THORSON 1946), are attached to the wadden bottom by a stalk fixed in the sand (fig. 21 A). According to the available literature, an egg-mass contains 400–1000 eggs, and in fairly good accord with this I found the following numbers of eggs or larvae in three egg-masses examined: 600–700 eggs, 1700–1800 eggs, and ca. 1000 larvae. As it is moreover known that a mature female contains 3000–5000 eggs, it must be assumed that it spawns several times (THORSON l. c.). In addition to the large spawning in spring, it would seem that a minor spawning may take place in the autumn, for in micro bottom samples taken on the wadden north of Fanø on $^{11}/_{12}$ 1946 a few quite small larvae were found, of the same size as those that are met with in May.

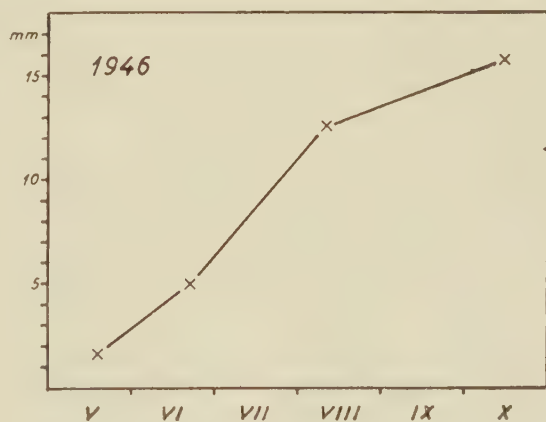
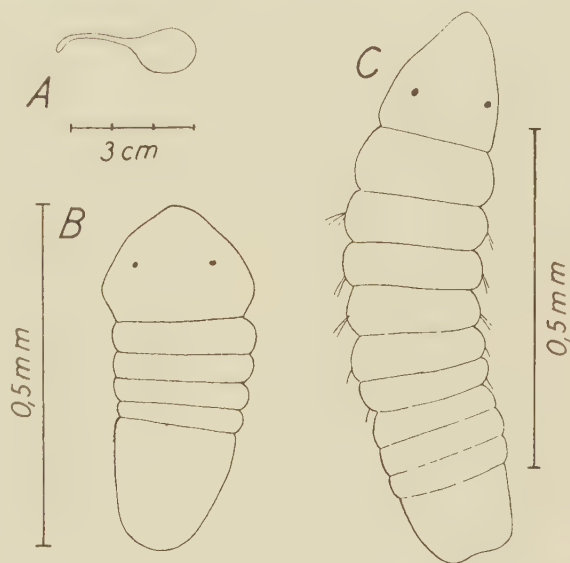


Fig. 21. *Scoloplos armiger*. Above: A. egg-mass. — B. Larva dissected out of egg-mass (drawn from preserved sample).—C. Larva from micro bottom sample (drawn from preserved specimen). — All from the sand wadden north of Fanø, $^{21}/_4$ 1946. — Below: growth curve for the 0-group in 1946 (see p. 54).

In agreement with the available literature (see THORSON l. c.), the development in the Waddensea, too, is non-pelagic. Fig. 21 B + C shows a larva dissected out of an egg mass and a young bottom stage from a micro bottom sample. The growth is shown in fig. 21 (below), which is based on the following numbers of individuals measured: $17 \cdot 18/5$ (102 individuals), $22/6$ (56), $10/8$ (14), $15 + 16/10$ (20). From the middle of May to the middle of October, 1946, the young grew from an average length of 1.6 mm to an average length of 15.8 mm. It will be seen from the curve that growth was most rapid in June–July. The average length for adult individuals in the same locality in October 1946 was ca. 5 cm (only 9 individuals measured).

2) Quantitative occurrence and mortality.—The 0-group was found on the wadden north of Fanø on $18/5$ 1946 to a number ranging between ca. 1000 and 12,400 per m², while about the middle of October the number ranged from less than 50 to ca. 230 per m². In 1948, in the same wadden area, 29,400 individuals per m² were found on $15/4$, but at the end of August the number had been reduced to ca. 2000. Thus, in both these two years only little more than 1 per cent. of the young of the spring was left, and this considerable reduction of 0-group ^{individuals} larvae in the course of the summer can only be due to persecution by enemies. The number of adult individuals varies greatly both in time and from place to place, but generally the number on the waddens ranges between 50 and 400 per m², and only in a few cases will more than 1000 individuals per m² be met with.

Pygospio elegans CLAP.

1. Egg- and larval development.—As to the biology of reproduction, this species exhibits an exceptionally great variation, for according to the literature, development with, as well as without, nurse eggs may take place; further, development with non-pelagic and pelagic larvae, and finally several pelagic larval types occur. In the Waddensea, however, neither nurse eggs nor a non-pelagic development have been observed.

SÖDERSTRÖM (1920) demonstrated a non-pelagic development by means of nurse eggs, each egg capsule being found to contain 50–60 eggs, of which only 7–9 developed, while the remainder served as food. However, SÖDERSTRÖM put forward the view that the species has a pelagic in addition to the non-pelagic development. Simultaneously with my investigations in the Waddensea, ERIK RASMUSSEN (results still unpublished) and THORSON (1946) made investigations on the reproduction of the species, and according to THORSON (l. c.) the main results of these investigations are as follows: Development both with and without nurse eggs has been ascertained, and in the plankton of the Sound THORSON found three different larval types, which he denoted A, B, and C. Of these, the A-larvae are assumed to have developed in egg capsules without nurse eggs, while the B- and C-larvae are regarded as developed by means of nurse eggs, and in addition the hypothesis is advanced that the capsules from which type B developed contained more embryos than the capsules from which type C developed, that is to say, that the C-larvae escape at a more advanced stage of development than the B-larvae.

In the Waddensea I have not observed development by nurse eggs; but in a few cases I was able to observe that all the eggs in the capsules developed into pelagic larvae. Larvae were observed in the plankton at all seasons of the year, and in the summer half-year they were present in considerable quantities. If development by nurse eggs takes place at all, it can only be of subordinate importance.

Egg capsules corresponding entirely to those described by SÖDERSTRÖM (l. c.) were found on several occasions in the tubes, in which they were ranged in rows, attached to the

wall of the tube by their adhesive stalk (fig. 22 A). The number of capsules per row was found to vary between 12 and 16, which is in good agreement with SÖDERSTRÖM's statements. But while SÖDERSTRÖM found 50–60 eggs per capsule, in the Waddensea there were only between 23 and 24, on an average (in 6 capsules examined the following numbers of eggs were found: 25, 25, 18, 16, 24, and 21, and in four other capsules the following numbers of unhatched

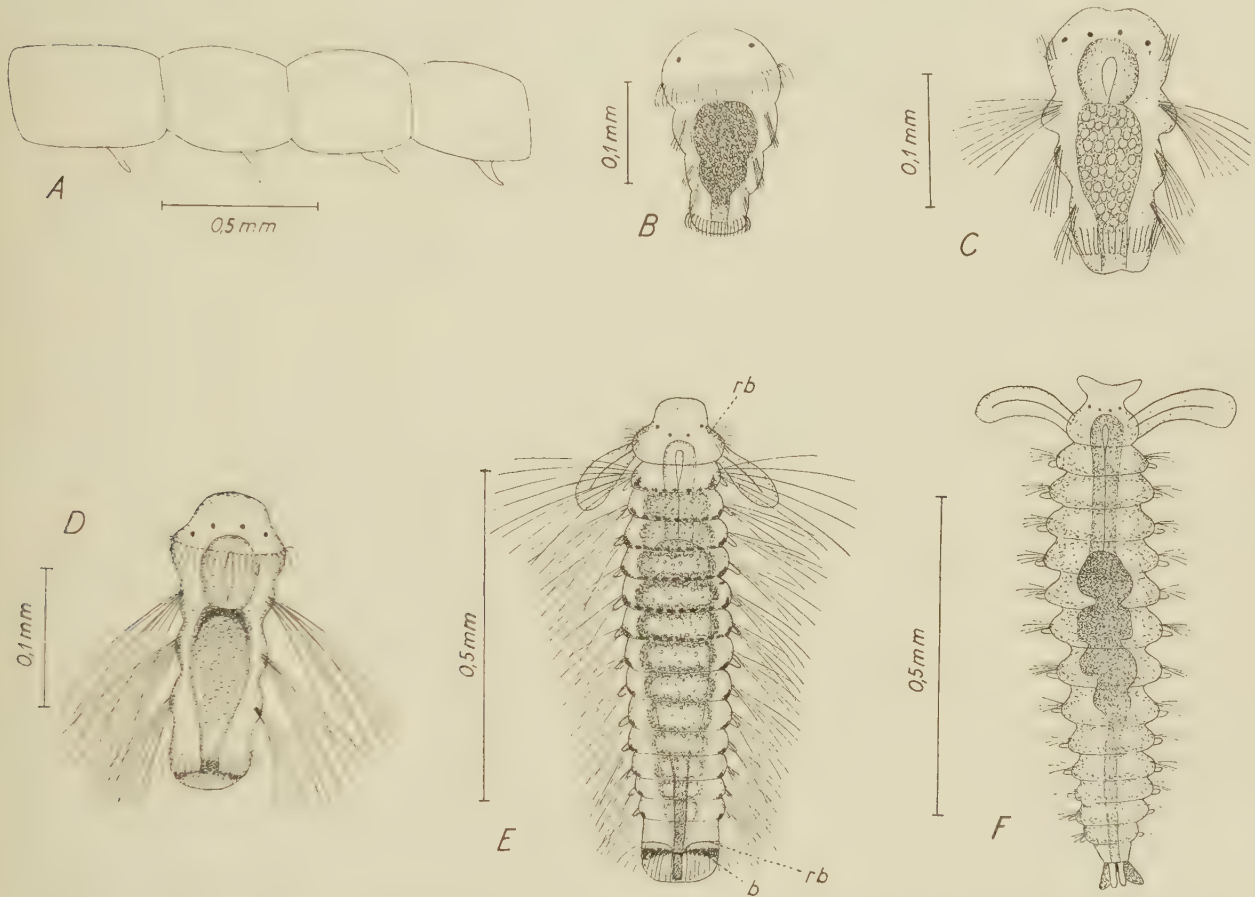


Fig. 22. *Pygospio elegans*. A. egg-capsules. — B. Larva dissected out of egg capsule (material collected on the sand wadden north of Fano $5/9$ 1945, drawn preserved). — C. Larva swimming out of tube (collected on the wadden northeast of Fano $25/7$ 1944, drawn from life). — D. and E. Younger and older larvae of type I from plankton off Esbjerg, taken $24/7$ 1944 and $5/8$ 1943, respectively (drawn from life; b = black, rb = reddish-brown pigmentation). — F. Newly settled stage of type I (settled in the laboratory on $4/8$ 1943).

larvae were found: 27, 28, 23, and 25). Thus there are 300–400 eggs per chain of tubes. All the egg capsules examined were taken in the period July–September, but since larvae of all sizes are present in the plankton at all seasons of the year, it must be possible to find eggs, too, all the year round. Still the summer half-year (April–October) is the most productive period.

In the capsules the eggs develop into larvae with three chaetigerous segments. In a material collected on the wadden north of Fano on $6/9$ 1945 an egg capsule chain was found to contain a little over 300 not yet fully developed larvae (fig. 22 B), all at the same stage of development: they were colourless and their intestine was filled with yolk; they had three

chaetigerous segments, but all setae were still entirely enclosed in the body-wall; further, one pair of eyes and two ciliated bands (one on the foremost and one on the hindmost segment). In fresh material collected on the wadden at Fano on $^{25}/_7$ 1944 a swarm of larvae was found in a tube; they had left the egg capsules and were now swimming out into the water (fig. 22 C). The tube further contained two adult *Pygospio*, which by their movements pumped the larvae out into the free water masses. The larvae differed from those described above by a greater differentiation of the intestines, by the setae having grown out, and by having two pairs of eyes. A number of 141 larvae were found in the tube, but a great many—probably more than half the number—had already left the tube and the majority had disappeared among the other material of tubes in the glass vessel.

The youngest larvae present in the plankton have three chaetigerous segments and on the whole entirely resemble the larvae that were observed to swim out of the above-mentioned tube. But from this stage the development proceeds in three different directions, the plankton containing three different larval types, I, II, and III, which I first took to belong to three different species, but which, in the glass dishes, all metamorphosed into bottom stages of *Pygospio elegans* (each type being placed in its own dish).

Type I (fig. 22 D + E) is comparatively short and broad, and the large larvae in the plankton, before settling on the bottom, attain a length of 0.7–0.9 mm. The number of chaetigerous segments before settling is 13–16, and in a few cases (in the substratum experiments described below) larvae were seen to settle with 11 and 18 chaetigerous segments. On the head a pair of tentacles, two pairs of eyes, and a prototroch are seen; on the body segments there are long larval bristles, which are discarded on metamorphosis and replaced by shorter bristles, which are already present in the largest larvae; finally, a telotroch is found. Pigmentation: In the body wall there is a peculiar scattered black pigmentation, which seems to be located on the inner side of the wall of the body cavity; in addition, transverse rows of small black pigment dots are found, more or less distinctly on the dorsal side of a number of the segments; an intense black pigmentation is seen in the last segment behind the telotroch, and finally, a very faint black pigmentation is found in the pharynx, and a somewhat stronger one in the intestine near the anus. A brown pigmentation is visible along the two ciliated bands. The oldest planktonic larvae develop a pair of appendages on the dorsal side of the last segment, and at the same time the segment itself begins to split towards the median plane; in this way the four anal appendages, so characteristic of the bottom stage, are formed. From the large larvae the type can be followed through the younger stages with three chaetigerous segments, but of the easily recognisable characters of the older larvae, only the strong black pigmentation behind the telotroch and the black pigmentation of the intestine near the anus are developed at this stage.

Type II (fig. 23) is somewhat larger than type I, since before settling it attains a length of over 1 mm and a number of at any rate 17 chaetigerous segments. It differs from the preceding type in the pigmentation. Most readily recognisable is the larva with two rows of black pigment spots along the dorsal side (one pair of spots per chaetigerous segment with the exception of the first one). Further, there is a faint black pigmentation of the last body segment and a fairly intense black pigmentation of the pharynx. As in type I, there is a brown pigmentation along the ciliated bands. At a cursory glance it may resemble the larva of *Polydora ciliata*, but is easily distinguishable from this latter by the bristles on the fifth chaetigerous segment not differing from the others, and by the absence of the star-shaped pigment between the eyes. In the plankton the larvae can be traced to quite small sizes (in some cases down to the stage

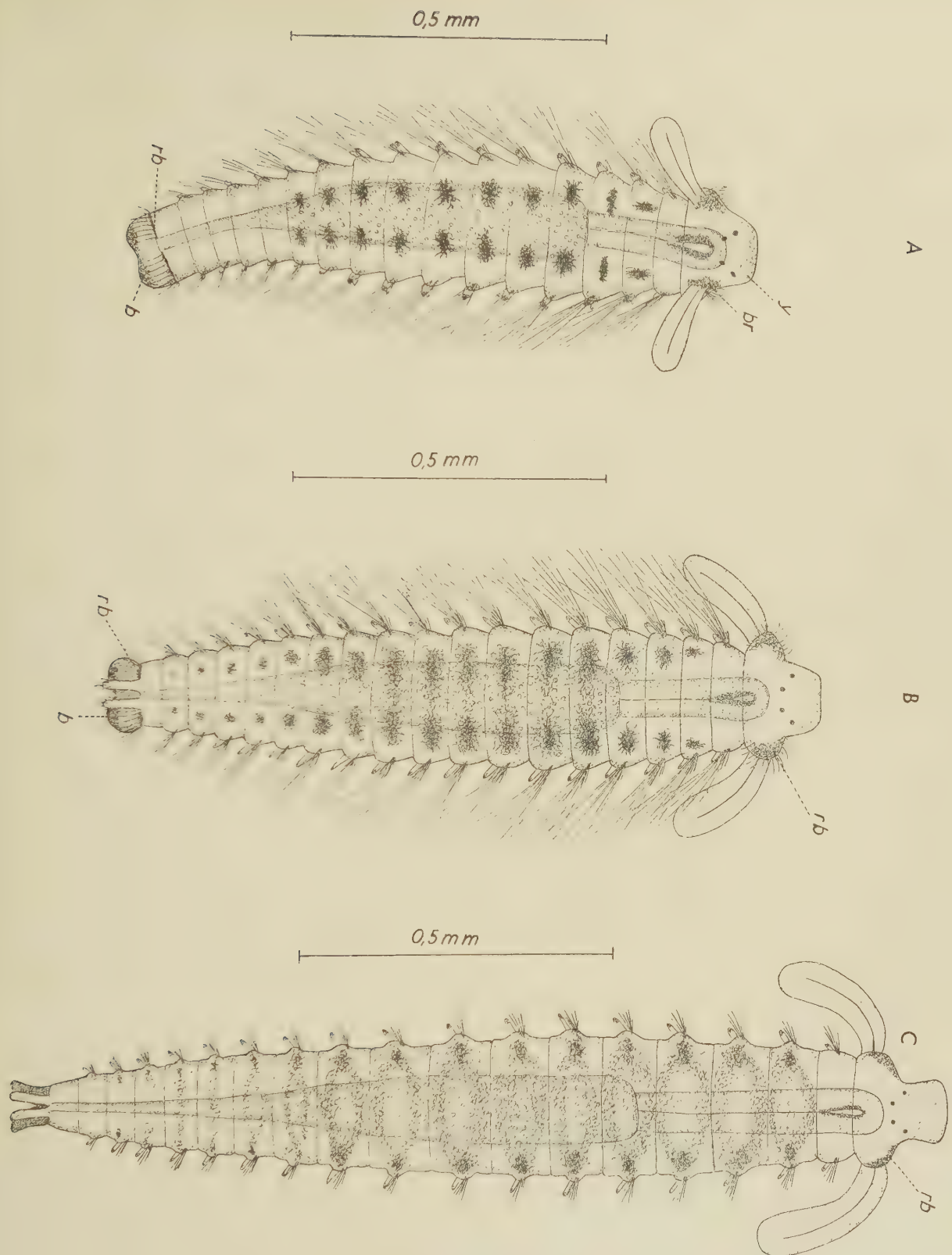


Fig. 23. *Pygospio elegans*, larval type II. A and B. Young and older stages from plankton taken off Esbjerg on $29/7$ and $5/8$ 1943, respectively. — C. Newly settled stage (settled in the laboratory on $9/8$ 1943). — (All drawn from life; b = black, br = brown, rb = reddish-brown, and y = yellow pigmentation.)

with three chaetigerous segments), being always recognisable by the black pigment spots on the dorsal side. The four anal appendages of the bottom stage are initiated in the same way as in type I.

Type III (fig. 24) is that which attains the greatest length as a pelagic larva, since it may be over 2 mm long and may develop 20 chaetigerous segments, but then it has, in fact, partially metamorphosed, the long larval bristles having been thrown off and replaced by the shorter ones. Larval bristles are found in the younger stages, at any rate till they attain a length

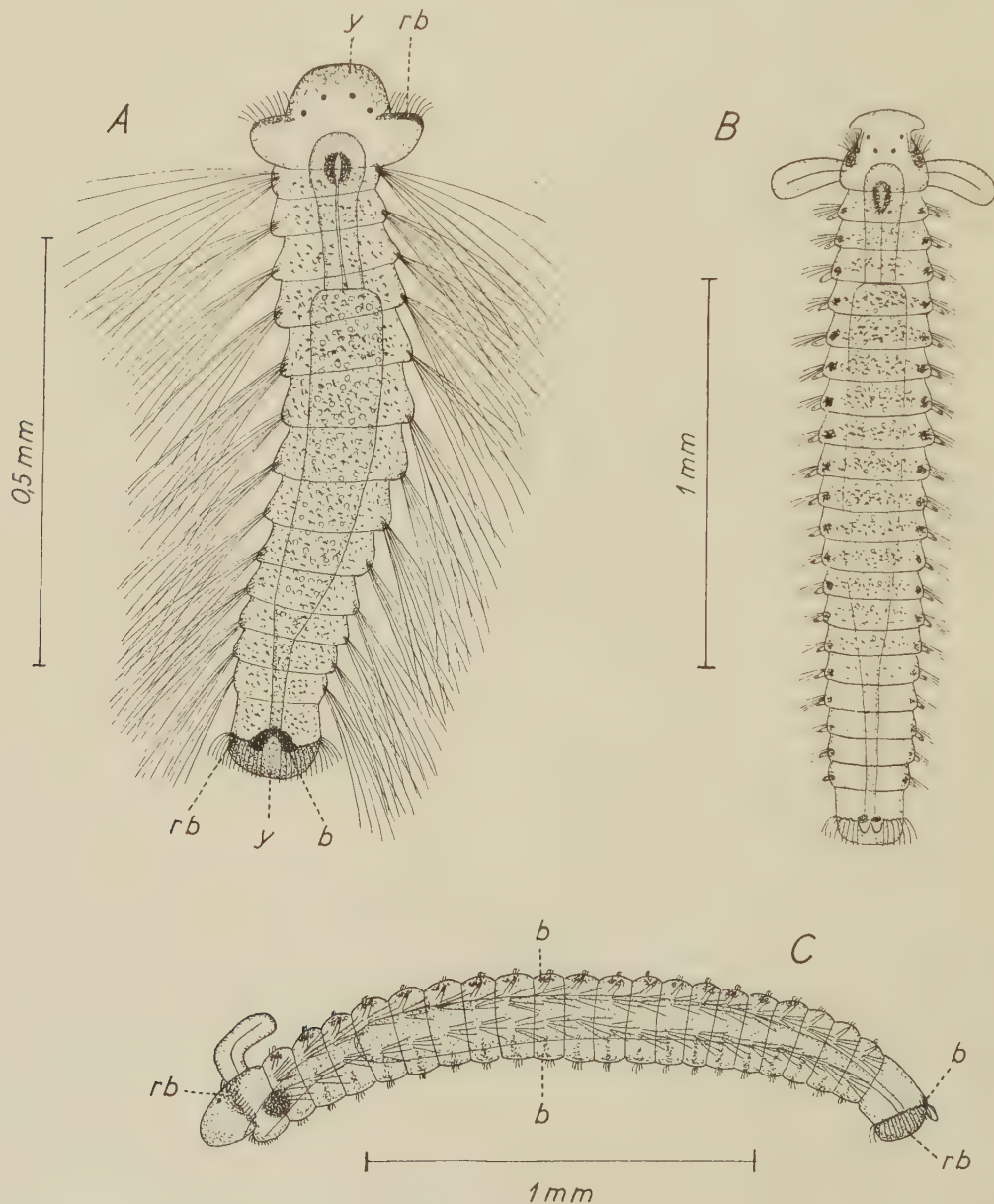


Fig. 24. *Pygospio elegans*, larval type III. A. Young stage, B and C older stages. All from plankton taken off Esbjerg in July 1942. (All drawn from life; b = black, rb = reddish-brown, and y = yellow pigmentation.)

of 0.75 mm. In this type the pigmentation is much fainter than in the other two: On the dorsal side there is a very faint scattered black pigmentation, while in the pharynx a distinct black pigmentation is seen, and on the dorsal side of the last segment there are two distinct black pigment spots, which are connected with each other, and behind which the two dorsal anal appendages are developed. Brown pigment is found along the ciliated bands and scattered on the ventral side; further, the two pairs of eyes are reddish brown. Anteriorly on the prostomium and posteriorly on the anal segment some yellow pigment is seen. In the plankton the larvae could be followed down to the stage with three chaetigerous segments (recognisable by the black pharyngeal pigment and the otherwise very faint pigmentation).

The three types are generally easily distinguishable, but sometimes transitional specimens occur which cannot with certainty be referred to any of the types. Thus in some cases it may be difficult to decide whether you have a specimen of type I or type II before you, and in other cases whether it belongs to type II or type III. It is often impossible to divide the youngest stages (with three chaetigerous segments) into types.

On comparing these types with the types erected by THORSON (1946), a fairly close similarity will be seen between THORSON's type C and my type I, and between THORSON's type B and my type III. As already mentioned, THORSON thinks that the different types have arisen by the individuals having left the egg capsules at different stages of development according to the quantity of food that was present for them; however, this hypothesis is not applicable to the types found in the Waddensea, as they all begin their pelagic life at the same stage.

Counting of the larvae in the plankton samples revealed distinct differences in the occurrence of the three types. All the larvae counted were distributed as follows over the low-water and the high-water samples:

	high-water	low-water
Type I.....	40 %	60 %
— II.....	64 —	36 —
— III.....	98 —	2 —

Type I is generally a little more frequent in the low-water samples than in the high-water samples. In about half of the days of sampling it was most frequent at high-water and on the other half it was most frequent at low-water. It was taken on altogether 44 days of sampling (in all the months of the year, but most frequently in the summer half-year), and the maximum number was 2400 individuals per m³ of water (low-water sample ²²/₅ 1947). Type II, on the other hand, is generally somewhat more frequent in the high-water samples than in the low-water samples. It was taken on 15 days of sampling (in the period May—October), on 13 days of which it was most frequent at high-water. The maximum number was 136 individuals per m³ of water (high-water sample ²⁹/₈ 1943). Type III was far more frequent at high-water than at low-water. It was counted on 24 days of sampling (in the period April—October), on 23 days of which it was most frequent at high-water. The maximum number was 346 per m³ of water (high-water sample ²⁰/₄ 1943). From these facts it can be concluded that type I is mainly produced in the Waddensea, while there is a great probability that the other two are chiefly produced outside the Waddensea, or in its outer area; this applies especially to type III.

2) Settling. Passing from the pelagic into the bottom stage, the larvae change in various ways. From being swimming animals, they now become creeping, and build tubes of available

bottom material (sand or mud particles). If suitable bottom material is lacking, they may possibly form only slime tubes. Simultaneously with the change in their mode of living, the animals undergo a metamorphosis; they grow longer, the four anal appendages are developed, and the ciliated bands and the larval bristles disappear. Newly settled larvae, which have formed tubes but have not yet metamorphosed, are at a creeping-swimming stage, being capable of swimming up again into the free water masses.

In a number of experiments it was shown that the settling is furthered by the presence of a natural substratum, while the lack of such a substratum will prolong the pelagic life. The experiments were made in the following way: A number of larvae which had attained such a size that they were near settling, were pipetted out of fresh plankton samples and distributed in glass vessels with different substrata or without any substratum. If it was not possible to secure a sufficient number of larvae at precisely the same stage of development, care was taken that the stocks in the different vessels within the same experimental series should be of the same composition. In order that there may only be a small quantity of substratum as compared with the quantity of water above, glass vessels with a pointed bottom will be the most suitable, and small wine-glasses holding about 30—40 cm³ proved convenient for this purpose. Only larvae of type I were used, and a total of 683 larvae were employed in the 12 experimental series. No experimental series gave conflicting results; but in two series, in which the larvae had been kept in the laboratory for nine days before the experiments were started, they were very little inclined to metamorphose. In some cases the death-rate among the larvae was rather high. The most typical and instructive experiments will be dealt with below. As substrata the following substances were used: sand from sand waddens (S), mud from soft waddens (M), mixed mud and sand (S + M), pebbles (of pea-size) from the wadden (St.), sterile sand (strongly heated and treated with acid) (st. S). The results are represented in curves, which show the percentage quantity of the settled larvae.

Experimental series 1 and 2 (fig. 25¹⁺²).—Arrangement: in both series a vessel with a mixed substratum (S + M) and one without any substratum (S) were used. In the first series the experiments were started with 15 larvae in each vessel, in the second series with 22 larvae in the vessel with a substratum and 18 larvae in that without any substratum. Result: In the vessels with a substratum the settling percentage was high, while it was diminutive or nil in the vessels without a substratum.

Experimental series 3 and 4 (fig. 25³⁻⁴). Arrangement: In both series one vessel with pure sand (S), one with mud (M), and one without a substratum (0) were employed. Twenty larvae were placed in each vessel. Result: Both series showed that settling is furthered by naturally occurring sand as well as mud, while it is impeded by the absence of a substratum, as in the first two series.

Experimental series 5 and 6 (fig. 25⁵⁻⁶).—Arrangement: In series 5 vessels with sand (S), mud (M), and sterile sand (st. S), and in series 6 in addition vessels without a substratum (0), were employed. In series 5 each vessel contained 18 larvae, in series 6 the vessel with mud contained 22 larvae, while each of the other vessels contained 20 larvae. Result: As in the preceding series, both wadden-sand and mud proved to stimulate settling, while sterile sand seemed to have a very slight or no effect. In series 6 larvae in vessels with sterile sand and in vessels without a substratum kept swimming until October 2. (In the vessel with sterile sand there were 17 swimming and 2 settled larvae, while in the vessel without a substratum there were 17 swimming and no settled ones. During most of the time the larvae were seen to swim briskly about, to take in food particles, and apparently they grew slightly in size).

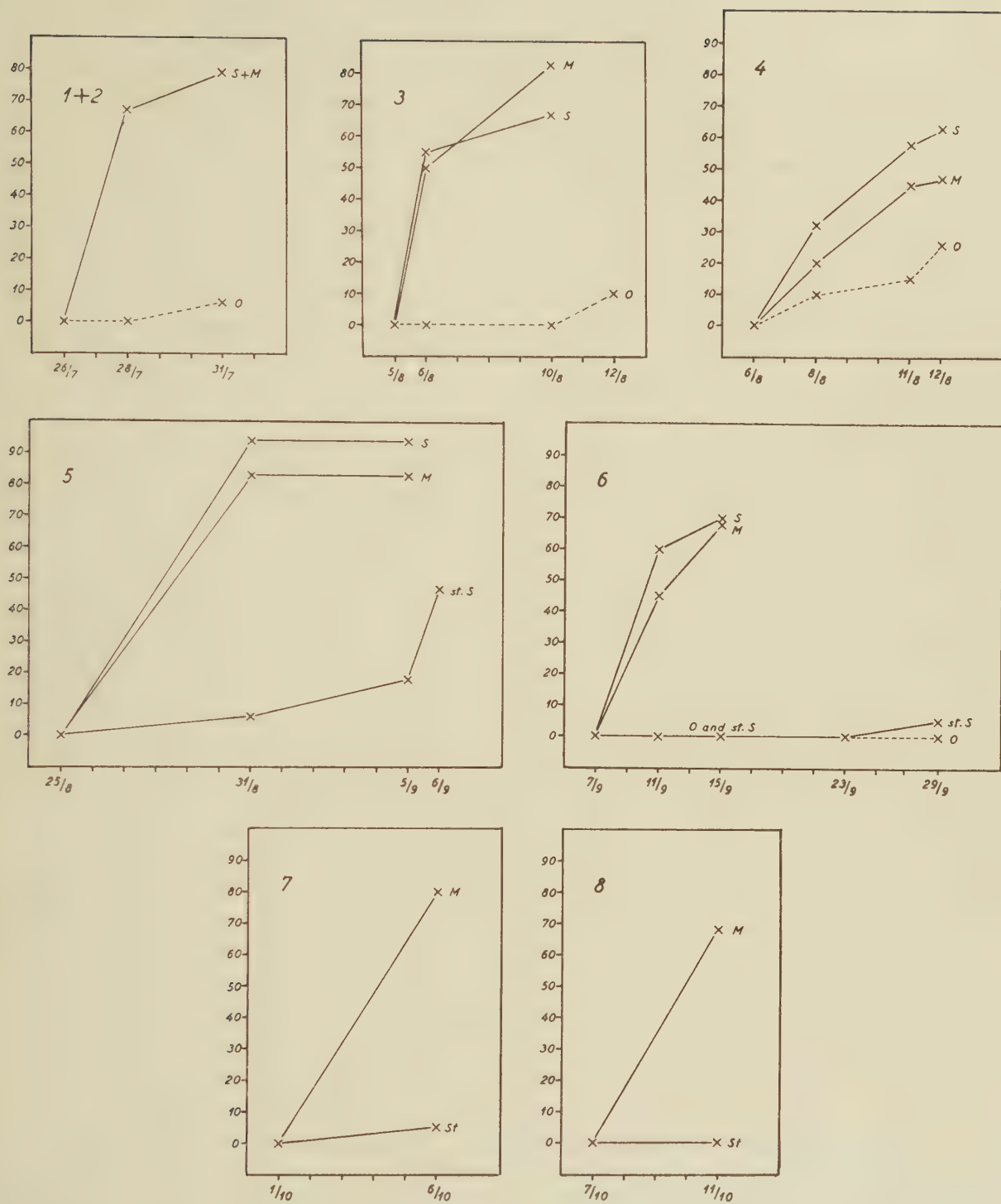


Fig. 25. *Pygospio elegans*. Substratum experiments, series 1—8. On the ordinate axis the percentages of metamorphosed larvae, on the abscissa the dates for the start of the experiment and dates for inspection of the larvae are indicated. (M = mud, S = sand, st. S = sterile sand, and O = no substratum). See the text on p. 60.

Experimental series 7 and 8 (fig. 25⁷⁻⁸).—Arrangement: In both series the effects of mud (M) and pebbles (St) were compared. Twenty larvae were transferred to each vessel. Result: While mud, as in the previous experimental series, had a highly stimulating effect on the settling of the larvae, hardly any settling took place in the vessels with pebbles as a substratum.

Experimental series 9.—On September 7th 20 larvae were placed in a vessel with mud, 21 larvae in a vessel with sand, and 20 larvae in a vessel with no substratum. On September 11th 17 larvae had settled in the first vessel, 12 in the second one, while in the vessel without any substratum all the larvae were still swimming. Then the experiments with a substratum were stopped, while that with no substratum was continued till October 13th, when the vessel contained 11 swimming and one settled, but not metamorphosed, larva. Thus these eleven larvae in the vessel with no substratum had kept swimming in the vessel for 36 days.

Experiment 10.—Twenty-one larvae, caught on September 2—3, were placed in vessels with no substratum. As late as November 4, that is, after two months had elapsed, the vessel still contained 14 unmetamorphosed swimming larvae, which, however, seemed to thrive poorly (kept on swimming along the bottom, were thin and elongate). In addition two dead unmetamorphosed larvae were found.

The results of all these experiments can be summarised as follows: A natural substratum (sand and mud) stimulates metamorphosis, while the lack of a substratum will impede it. Further, pure sterile sand and naturally occurring pebbles have an impeding effect. As naturally occurring wadden sand is always mixed with some mud particles and organic particles, it is possibly the presence of these which is of importance for the settling and metamorphosis of the larvae. Larvae kept without any substratum had not yet metamorphosed after two months.

3) Growth, quantitative occurrence, and death-rate.—Newly settled animals seem to grow rapidly (observations in the laboratory, figures in support hereof not available), and probably they will reach the mature size in the course of a few months. As the production of brood is very considerable (many larvae in the plankton during the greater part of the year), and since, owing to the effect of the substratum, large-scale settling must be assumed to take place all over the waddens, the death-rate of the youngest bottom stages, considering the very slight density of adult individuals over the greater part of the wadden, must be high. Some figures for the newly settled and older individuals (number per m²) from the sand wadden north of Fanø (160—170 m from the low-water mark) for the season of 1946 are given below:

Date	Newly settled animals	Older animals
22/6—26/6	31,500	400—500
2/8—10/8	18,000	—
8/9—10/9	8,400	—
15/10	—	100

The figures for the newly settled animals do not represent a single time-limited settling, but a settling persisting throughout the season, so the consumption of newly settled animals is considerably greater than is immediately apparent from the figures. Further, the circumstance that these newly settled animals will not be of noticeable importance as older individuals (they are not, or but sparsely, present in the macro bottom samples), shows that they are rapidly consumed.

Generally the quantity of older animals is largest on the inner parts of the waddens (in accordance with the observations of THAMDRUP (1935)). On the sand wadden north of Fanø the following numbers per m² were found nearest the shore: in 1946: $^{22}/_6$ — $^{26}/_6$ 2,500, $^{15}/_{10}$ 2,100; in 1947: $^{29}/_5$ 4,300, $^{22}/_7$ 100—200, $^{29}/_8$ 200—300, and $^{10}/_{10}$ 200—300. It will be seen that the quantity was much larger in 1946 than in 1947, which may be explained by the aforementioned abundant settling of young in 1946. On the wadden at Skallingen THAMDRUP (l. c.) found very large numbers in the inner wadden zone (maximum ca. 20,000 per m²).

Polydora ligni WEBSTER (= *P. ciliata* JOHNST.?)

It is mentioned in chapter VI that *Polydora ligni* is of common occurrence in the Waddensea and that, according to WÖHLENBERG (1937), it forms very dense populations in certain localities. Since, however, the larvae occurring in the plankton entirely resemble the larvae of *P. ciliata*, the question arises whether we are not concerned, here, with only one species with a certain range of variation.

1) Larval development.—Egg capsules were not observed on the material collected within the area dealt with; but the pelagic larvae (fig. 27 A + B) are exceedingly common in the plankton, and they correspond entirely to the larvae of *P. ciliata* described and figured by LESCHKE (1903), WILSON (1928), and THORSON (1946) (black star-shaped pigment between the eyes, dark pigment on the cheeks, and faint dark anal pigment). These larvae were reported by HAGMEIER & KÄNDLER (1927), also, to be very common in the plankton of the Waddensea. Their occurrence in the plankton of the Waddensea agrees closely with their occurrence in the Bay of Kiel (LESCHKE l. c.), the Sound (THORSON l. c.), and the harbour of Copenhagen (SMIDT 1944 A), being found in the plankton during nearly all the months of the year, though with their main occurrence in the period April—October and with a maximum occurrence in August or September. The maximum numbers (individuals per m³ of water) were as follows in the various years: September 1942: 1480, August 1943: 1445, August 1944: 2820, and August 1947: 1650. All these maximum numbers were found in samples taken at low-water. The counts showed that in the productive part of the year (April—October) the numbers are in most cases largest for samples taken at low-water, while the opposite is the case in the spring. Of all the larvae counted, ca. 77 per cent. were taken at low-water, which must mean that the greater part of the production of larvae had taken place in the Waddensea itself; some figures will further illustrate this:

Average number of larvae per m³ of water:

Year	High-water	Low-water
1942	125	346
1943	72	285
1944	113	479
1947	220	661
Average for all four years	132	443
	(23 %)	(77 %)

2) Settling of the larvae.—In a number of experiments it has been shown that the larvae, like larvae of *Pygospio elegans*, are stimulated to settle by the presence of a natural bottom substratum. The experimental technique employed was the same that was used for

Pygospio. A total of 338 larvae were used in eight experimental series, the most instructive of which will be recorded, the results being shown in curves indicating the percentage quantity of settled larvae.

Experimental series 1 and 2 (fig. 26¹⁻²).—Arrangement: In experimental series 1 a glass vessel with mud (M), one with sand (S), and one without any substratum (0) were

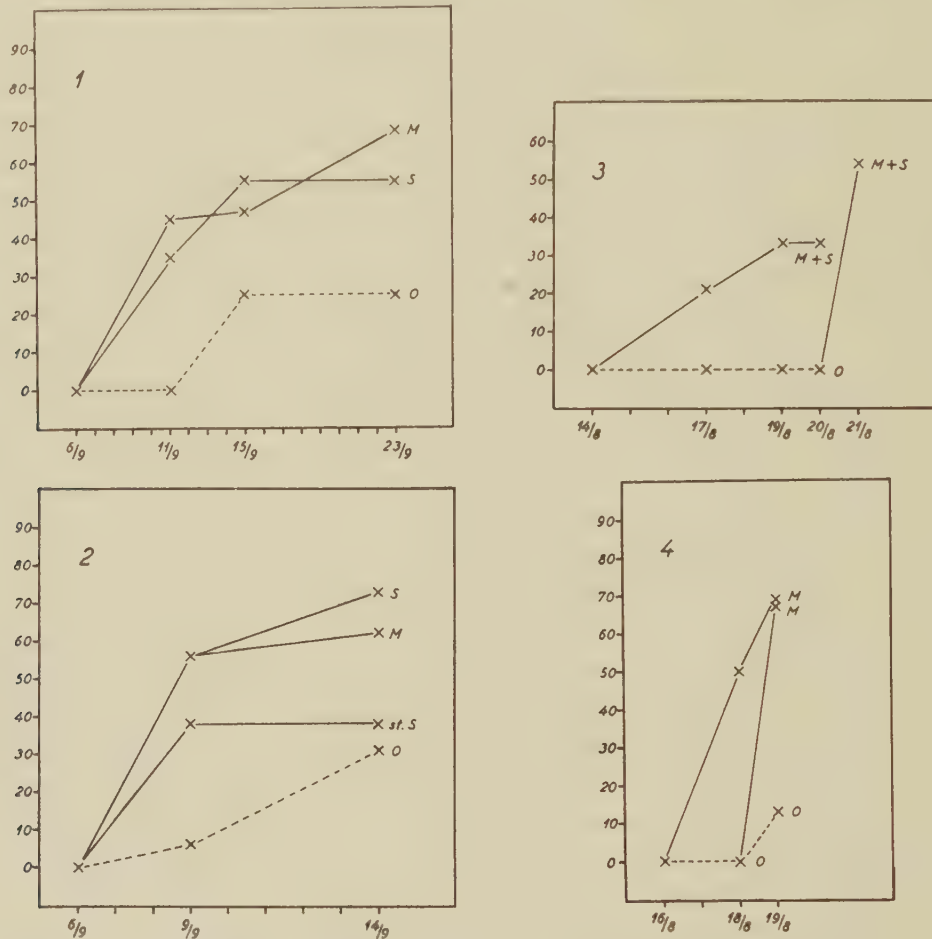


Fig. 26. *Polydora (ligni?)*. Substratum experiments, series 1—4. For explanation see fig. 25.

Cf. further the text on pp. 63—65.

employed. Twenty larvae were placed in each of the three vessels. In experimental series 2 a glass vessel with mud (M), one with sand (S), one with sterile sand (st. S), and one with no substratum (0) were employed. Fifteen larvae were placed in each vessel. Result: All the different kinds of substrata used furthered settling, while the absence of a substratum retarded settling without entirely preventing it. Sterile sand, however, seemed to have a slight effect.

Experimental series 3 and 4 (fig. 26³⁻⁴).—Arrangement: In experimental series 3 a vessel with a substratum mixed of sand and mud (M + S) and one which at first contained no substratum (0), but to which a mixed substratum (M + S) was later added, were employed. Fifteen larvae were placed in each vessel. In experimental series 4 a vessel with mud (M) and two vessels with no substratum (0), to one of which some mud (M) was later added,

were used. Sixteen larvae were placed in the first-mentioned vessel, fifteen in each of the other two. Result: Like the two preceding series, these two experimental series showed that the lack of a substratum will impede settling, but that the addition of a substratum will soon further the settling of the larvae.

Two more experimental series (with 11 and 20 larvae, respectively, in each vessel) showed distinctly that mud furthers settling, while the lack of a substratum impedes it. Finally, one experimental series showed hardly any inclination of the larvae to settle irrespective of the presence or absence of a substratum, and another series showed practically the same inclination of the larvae to settle whether or not a substratum was present.

Summing up the results, however, we can say that the substratum has a distinct effect, though it is less marked than in the case of *Pygospio*; thus it must be pointed out that the absence of a substratum has merely a retarding effect on the settling without entirely preventing it.

3) Quantitative occurrence.—While the species is of extremely sparse occurrence on the sand waddens, it is more abundant on soft and mixed bottom; however, very few exact figures to illustrate this are at hand. On the innermost part of the wadden north of Fanø (nearest the shore), where the bottom has a mixed character, ca. 900 individuals per m² were found on ²²/₇ 1947, but already on ²⁹/₈ the number had fallen to ca. 100 per m², and on ¹⁰/₁₀ only very few individuals occurred. In the same year ca. 400 individuals per m² were found on ²⁸/₈ on the soft wadden at Nordby (Fanø), but on ⁸/₁₀ none were observed in the samples here. This rapid reduction at the same time in two different localities must be assumed to be due to the persecution by enemies (possibly birds). In the samples collected in 1941 in the southern and middle parts of the Waddensea the density in the limited number of localities in which the species occurred, was ca. 50–100 per m², in a single case up to ca. 1600 per m². Considering the abundance of larvae in the plankton samples, remarkably few adults occur in the bottom samples. Presumably a number of localities with dense stocks are to be found in the less thoroughly investigated soft waddens or in shallow-watered channels, corresponding to those found by WOHLBERG (1937) and LINKE (1939) in the German Waddensea, only their presence has not yet been ascertained.

Heteromastus fliformis (CLAP.).

1) Reproduction.—No information about the spawning is available from the Danish Waddensea. According to LINKE (1939), the spawning takes place early in spring in Jadebusen, sexually mature animals being met with in winter and early spring, while in May they have no eggs.

The larvae have not previously been described in the literature. The larva shown in fig. 27 C, D, E, may belong to this species, as it is rather common in the plankton, and the adults are rather common on the waddens. These larvae, which have been found at various stages of development, are dark and opaque and provided with ciliated bands. Judging by their appearance, the larvae are lecithotrophic (a term used by THORSON (1946) for larvae which do not take in food, but subsist on their store of yolk). The presumed *Heteromastus* larvae were found in plankton samples taken off the harbour of Eshjerg in March, April, July, August, October, and December, but only in March–April and October were they found fairly frequently. In addition they were found in plankton samples taken at high water over the sand waddens north and northeast of Fanø in April, October, and November. Thus they seem principally to occur in spring and autumn.

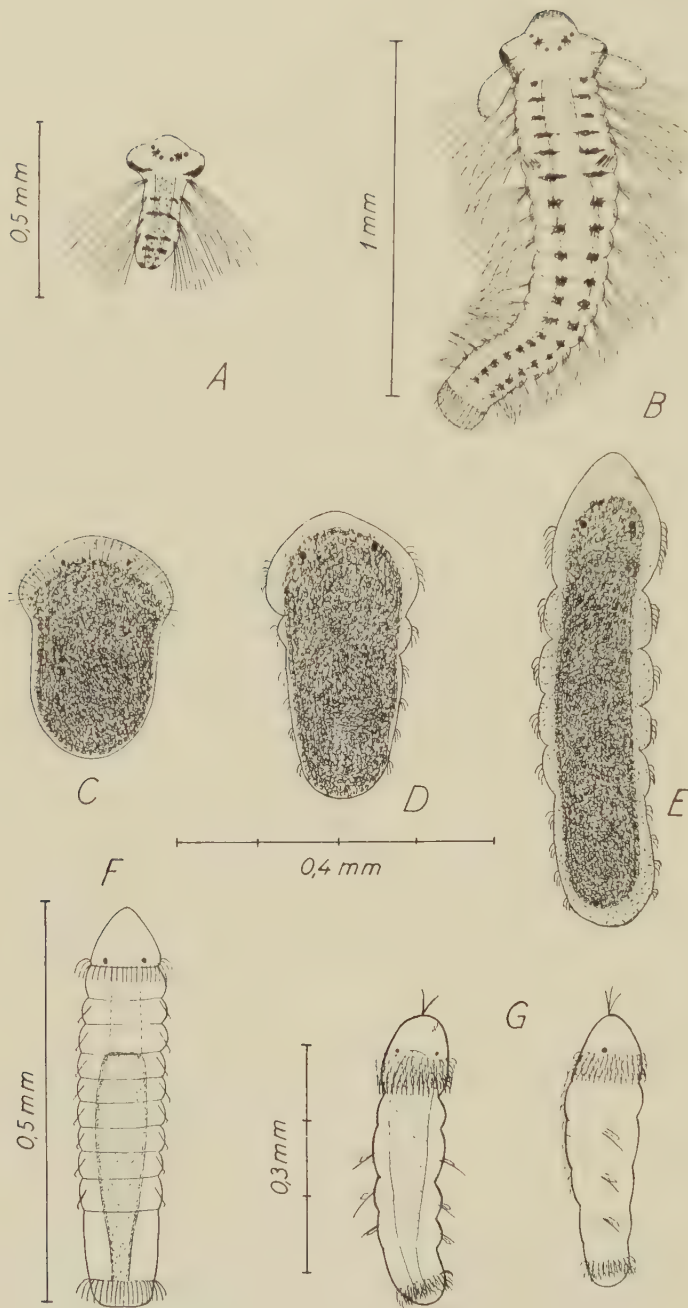


Fig. 27. A and B: Young and older larval stage of *Polydora (ligni?)* from plankton taken off Esbjerg on $2/7$ 1942 (drawn from preserved specimens). — C, D, and E: Stages of lecitotrophic Capitellid larva, possibly *Heteromastus filiformis* (C from plankton off Esbjerg $2/11$ 1942, D and E from plankton over the wadden north of Fanø $21/10$ 1946, all drawn from life). — F: Larva of *Capitella capitata* from plankton taken off Esbjerg on $8/8$ 1946 (drawn from life). — G: *Arenicola marina*. Larvae whirled up in the water over the wadden north of Esbjerg, $27/8$ 1943 (drawn from life).

2) Quantitative occurrence.—This species seems decidedly to be the most frequently occurring Capitellid on the waddens; but, as stated by THAMDRUP (1935), its occurrence does not seem to be very constant. In most samples it is present in numbers less than 100 per m^2 , but now and then it has been found in rather considerable numbers. Thus in the course of the summer and autumn of 1947 it was found in constantly increasing numbers on the sand wadden north of Fanø: on $22/7$ it was only found at a single station in numbers less than 100 per m^2 , on $29/8$ it was found on a large part of the wadden in numbers ranging between ca. 100 and ca. 350 per m^2 , and on $10/10$ it occurred all over the wadden in numbers between ca. 100 and ca. 2200 per m^2 , nearly 75 per cent. of which were young individuals. In the same year, on $28/8$, it was found on the mud wadden at Nordby (Fanø) to a number of ca. 800 per m^2 .

Capitella capitata FABR.

1) Larval development.—As regards egg-laying, no observations are available from the Waddensea; but EISIG (1887 and 1899) observed brood protection at Naples, the eggs being laid in the tube of the mother animal.

The larvae (fig. 27 F), which have been described and figured by a great many authors (cf. THORSON 1946), were found in small numbers in the plankton samples taken off the harbour of Esbjerg in the months of June, August, September, October, and November, most abundantly in August—September. They seem to occur with equal frequency in the plankton at low-water and at high-water. In ad-

dition some specimens were taken in plankton over the sand wadden northeast of Fanø on $9/10$ 1947.

2) Quantitative occurrence.—The adult bottom stages were taken in several places in the Waddensea, but only in small numbers as compared with *Heteromastus* (hardly ever in numbers exceeding 100 per m^2). Owing to the poorness of the available material, however, it is impossible to give exact figures.

Arenicola marina L.

In addition to my own observations I have to a certain extent used information acquired by conversations with worm-diggers and with Mr. A. C. CHRISTENSEN, worm-exporter at Esbjerg. I thought that these data could be used if they were in accord with my own experience or if—given independently of each other—they agreed mutually.

1) Spawning.—The development of the sexual products takes place in the summer and late summer, during which period the spawning is inconsiderable, the main spawning taking place in the autumn. The worms containing sexual products are swollen and are called “milk worms” by worm diggers because the sexual products flow out like a milky fluid when the worms are broken into pieces. The “milk” of the female individuals is yellowish, and the individual eggs are just visible as small yellow dots. The “milk” of the male individuals is a whitish sperm. The *Arenicola* stocks of the waddens include equal numbers of ♀♀ and ♂♂, for of 302 sexually mature worms examined 50.7 per cent turned out to be ♀♀ and 49.3 per cent ♂♂. At different times of the year the following numbers of worms were examined for their contents of sexual products: 1946: $17/12$ (50); 1947: $5/4$ (100), $23/4$ (75), $19/5$ (98), $22/5$ (68), $27/5$ (78), $15/6$ (110), $20/6$ (164), $22/7$ (106), $27/9$ (100), $10/10$

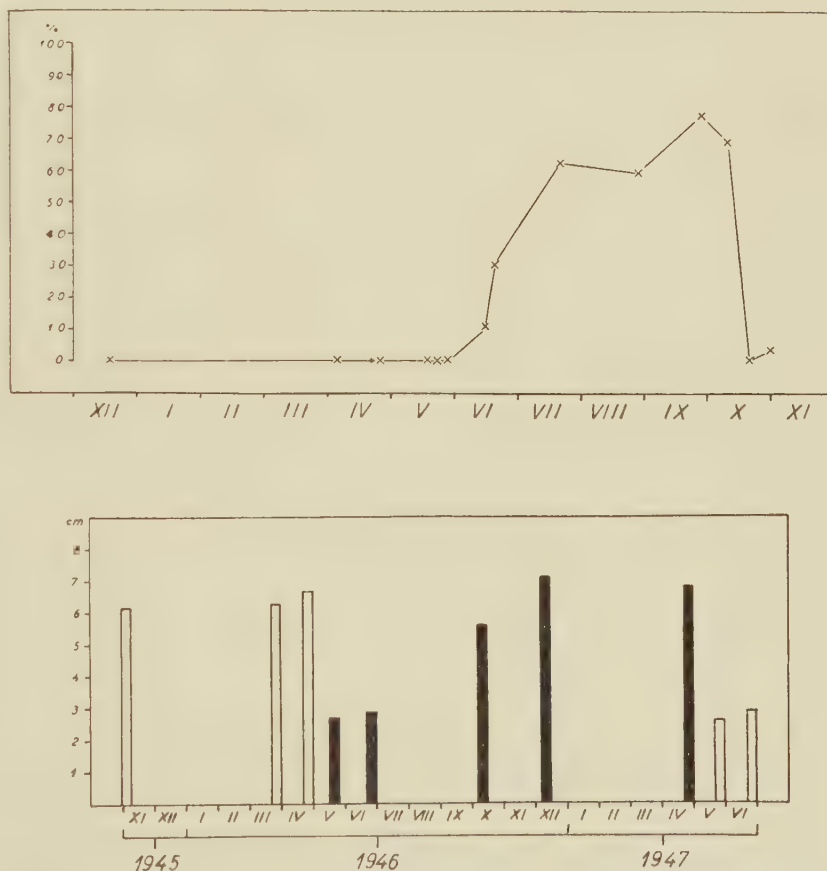


Fig. 28. *Arenicola marina*. Above: the percentage of sexually mature individuals of the adult population at different times during the period December 1946—October 1947. — Below: the average lengths, at different times of the year, of the smallest individuals forming visible excrement heaps on the wadden (white columns to the left representing year-group 1944, black columns year-group 1945, and white columns to the right year-group 1946).

(83), $^{25}/_{10}$ (100), $^{30}/_{10}$ (135). The result is illustrated in fig. 28 (above), which shows the percentage quantity of "milk worms" at the various dates. The curve shows that in winter and the months of spring no "milk worms" occur. They begin to occur in June and gradually increase in number during the following time (containing, at the same time, constantly greater quantities of "milk"). They attain their maximum occurrence at the end of September, which is followed by an abrupt decline towards 0, by which the large spawning is marked. In accordance herewith Mr. A. C. CHRISTENSEN (Esbjerg) reports that "milk worms" are especially found at the height of the summer and in the late summer. The above facts further agree with those recorded by the following authors, who state that the species spawns in the autumn: CUNNINGHAM & RAMAGE 1888, STORROW 1925, PIRLOT 1933, THAMDRUP 1935, THORSON 1946, NEWELL 1948. At variance with this, ASHWORTH (1904) states that mature sexual products have been found in February—April and in July—October.

As mentioned above, in addition to the large spawning in the autumn, some spawning takes place in the course of the summer. Thus a single *Arenicola* larva was found in a plankton sample as early as $^{17}/_6$ 1943, and in this connection I may mention that I found a few larvae in whirled-up bottom material from the Sound from the last days of June, 1947.

2) Larval development.—The larval development is practically non-pelagic or a very much shortened pelagic development; thus, in the many plankton samples collected at different seasons of the year in 1942, 1943, 1944, 1945, 1946, and 1947 *Arenicola* larvae were only found on very few occasions ($^{17}/_6$ 1943, $^{31}/_{10}$ 1943, and $^6/_{11}$ 1945) and only in a few specimens. On several occasions, however, from the end of August to the beginning of November larvae were taken over the sand waddens in whirled-up bottom material. Thus several larvae were taken with the plankton over a sand wadden north of Esbjerg on $^{27}/_8$ 1943 in a heavy swell, which whirled up a good deal of bottom material in the water. Further it may be mentioned that on the 4th and 5th of November, 1945, a considerable number of larvae were taken in whirled-up bottom material over the sand wadden north of Fano.

The following table 5 shows the results of the samplings for *Arenicola* larvae, carried out in whirled-up bottom material over the sand waddens at Fano and north of Esbjerg (0 = no larvae found, r = a few, + = some specimens, c = common):

Table 5.

March			April			May			June			July		
date	year	larvae	date	year	larvae	date	year	larvae	date	year	larvae	date	year	larvae
25	46	0	18	46	0	16	46	0	23	46	0	27	43	0
28	46	0	23	47	0	19	46	0	25	46	0	19	44	0
						23	47	0	18	47	0	31	44	0
												22	47	0
August			September			October			November			December		
date	year	larvae	date	year	larvae	date	year	larvae	date	year	larvae	date	year	larvae
27	43	+	26	43	0	21	46	0	4	45	c	31	45	0
18	44	r	5	44	0	9	47	0	5	45	c	10	46	0
28	44	0	7	44	0	11	47	0	7	45	0	11	46	0
9	46	0				29	47	r				14	46	0
29	47	r				30	47	+						

It will be seen that all the finds were made in the period from the last half of August to the beginning of November.

The larvae found (fig. 27 G) had from one to three chaetigerous segments and they showed good agreement with those published by BLEGVAD (1923) and NEWELL (1948 and 1949). On several occasions they were kept under observation in glass dishes with a natural substratum. In this way their mainly non-pelagic mode of living was confirmed, since for the most part they crawled about among the bottom material and only now and then took short swims with brisk movements, to seek the bottom immediately afterwards. Similar observations were made by NEWELL (1948). That the development is predominantly non-pelagic is further confirmed by the fact that other authors, also, have in vain searched for larvae in the plankton, viz. THORSON (1946), GUSTAVSON (verbal information, published by THORSON 1946), and NEWELL (l. c.). Thus all the above-mentioned facts invalidate the view put forward by THAMDRUP (1935) that the larvae live a pelagic life all through the autumn and winter.

The pelagic "Benham stage" was not observed in any sample from the Waddensea. THORSON (1946) thinks that this stage represents either newly settled larvae, which with their slime tube have been whirled up in the water by strong water movements, or individuals which have metamorphosed in "mid-water".

3) Post-larval stages.—In spite of extensive search in the autumn and winter it has not yet been possible to find the youngest post-larval stages on the waddens, that is, the stages intermediate between the larval stage with three chaetigerous segments and the youngest stage forming excrement heaps, which occurs in May. THAMDRUP (1935) did not succeed, either, in finding this stage, so he came to the conclusion that the brood was pelagic during the whole autumn and winter. Not till quite recently did NEWELL (1949) succeed in finding this intermediate stage, which in February 1949 had a length of 2.5—3.2 mm. The animals had a well developed caudal region and were enclosed in slime tubes. NEWELL gives some good figures of this stage, which differs in several respects from that found by THORSON (1946) in a "bottle collector" in the Sound (p. 109, fig. 59); NEWELL therefore thinks that THORSON's larva cannot be *Arenicola*. NEWELL found these youngest stages in the pebble and *Fucus* zone, whence they later (in May) spread over the tidal flat.

In May the young bottom stages have reached such a size that they are able to form excrement heaps on the surface of the wadden, so they are very easily found. Their average length at this time is 26—27 mm (varying between 13 and 39 mm in the material examined), and they differ from the older worms by not yet having developed gills. They are found in U-shaped tubes which extend into the bottom to a depth of 5—10 cm, and in these tubes the worms may crawl to and fro, up into both branches of the U, so in some cases the worm can be found with the posterior end upwards, in other cases with the anterior end upwards. This stage was not observed by THAMDRUP (l. c.) till the month of June, but by NEWELL (1948) in April.

4) Growth.—In fig. 28 (below) the growth of these young bottom stages is illustrated. The columns indicate the average lengths of the smallest worms forming excrement heaps, dug up at different times of the year. The measurements were made on individuals preserved in alcohol, and the following numbers were measured: 1945: November (35); 1946: March (23), April (34), May (60), June (50), October (36), December (18); 1947: April (16), May (42), June (32). The figure shows that the small individuals of *Arenicola* in the course of the summer and the autumn attain a size of 6—7 cm, when they are about one year old, after which, in the winter months, the growth is arrested, the average length being accordingly about the same in the autumn and in the succeeding early spring. It has, however, been impossible to follow the growth further, for in the course of the summer the worms reach the sexually mature size,

so they are no longer distinguishable from the older worms. Thus the development from the larval stage to an individual spawning for the first time takes two years, which is in perfect agreement with the investigations made by NEWELL (1948).

Measurements made of 565 worms dug out by worm-diggers north of Esbjerg on $18/4$ 1948 showed an average length of between 17 and 18 cm and a variation between 8 and 28 cm. However, the worms exhibit distinctly different average sizes on the different kinds of bottom, being largest on a coarse-grained, and smallest on a fine-grained bottom. In illustration hereof it may be mentioned that Mr. A. C. CHRISTENSEN, worm exporter, has informed me that, of worms dug out of the sand wadden northwest of Fanø 40—50 will constitute half a litre, while of worms from the mixed wadden south of Esbjerg as many as 125—200 will go to the $1/2$ l.

5) Quantitative occurrence and migrations.—As stated in the preceding chapter, the youngest bottom stages are chiefly found near the high-water mark or on other high-lying parts of the waddens, while the older stages prefer the lower-lying areas, a distribution that was also demonstrated by THAMDRUP (1935), WOILENBERG (1937), and NEWELL (1948 and 1949). In illustration hereof the subjoined table shows the distribution of 0-group and older individuals of *Arenicola* found on the wadden north of Fanø on $26/6$ 1946 along a sampling line from the shore to the edge of the wadden. The figures indicate the number of individuals per m^2 .

0-group stage	0	0	0	1.1	3.2	4.2	
Older stages	9.9	6.9	13.1	13.6	7.9	2.4	
Metres from the low-water mark	10	130	220	320	390	430	450 (shore)

The figures give no satisfactory information about the quantitative proportion between the young and the older stages, the young being inclined to congregate in patches. When the young grow up, they move to the outer part of the wadden, away from the high-water mark, probably by swimming, *Arenicola* being reported to have been observed swimming (EHLERS 1892, MEEK & STORROW 1924).

Other observations in nature, also, give evidence of migrations of the worms. Thus THAMDRUP (1935) states that wadden areas which have been emptied of worms by worm-diggers, may in the course of one month become inhabited by adult worms in the same numbers as before the digging. The aforementioned worm exporter, Mr. A. C. CHRISTENSEN, Esbjerg, and a worm-digger in Fanø have supplied the following particulars: The worms may be abundantly present in a place one day, and the next day one may dig for them in vain in the same locality. Further, the worms disappear from the upper part of the wadden when for some length of time the water has not been very high. Similar migrations were demonstrated by CHAPMANN and NEWELL (1949) in August 1948 by filling two excavations in the tidal area with sand containing no *Arenicola*, and afterwards keeping these excavations under constant observation. Gradually an immigration of *Arenicola* took place, especially in April 1949.

6) Mortality.—In the *Arenicola* stock the death rate seems to be low. If the mortality were high, the quite young individuals (the 0-group) might be expected to be much more numerous than the older age-groups; however, the opposite seems to be the case. As far as I am able to judge, several times as many *Arenicola* of the older age-groups as of the 0-group are present, which must mean that the majority of the stock will attain an age of several years. This assumption is further supported by aquarium observations made by THAMDRUP (1935), which show that *Arenicola* may attain an age of at least six years. The action of natural enemies

may perhaps bring about a decimation of the two youngest age-groups, small-sized whole *Arenicola* having in some cases been found in fish stomachs. The larger-sized *Arenicola*, also, are pursued by the bottom fishes (see chapter X), but since these generally bite off the posterior parts of the animals only, this will hardly mean any harm to the *Arenicola* population, the worms being capable of regenerating the bitten-off hind parts, as was shown experimentally by ORTON (1935) in nature. However, the intensive digging-out of *Arenicola* for bait in certain places may probably have a decimating effect in these places.

While under normal natural conditions a relatively low mortality among the adult *Arenicola* may be taken for granted, the more exceptional severe winters may kill many worms. Particulars concerning this point are available from the severe winter of 1947, when, according to the reports of the worm-diggers, the stock of worms had declined so much that many dead worms were found on the waddens or had been washed up on to the shore. But curiously enough it was also reported that already in May not only the same numbers of worms as in the previous year were present, they even considerably exceeded the numbers for the previous 2—3 years; this was confirmed by my samplings in June, as will be seen on comparing the subjoined figures with the figures on p. 70 (the figures indicate the quantity of young + older *Arenicola* per m² found on the wadden north of Fano on ¹⁹/₆ 1947 along a line between the shore and the edge of the wadden):

Numbers of individuals:....	18.5	23.8	28.5	22.7	7.0	3.9	4.5	
Metres from the low-water								
mark.....ca. 10	75	150	225	300	375	410	450 (the shore)	

The explanation of this very peculiar fact can only be that an immigration of worms has taken place from deeper water, where the stock had been spared during periods of frost. It must be admitted, however, that as regards the peculiar fluctuations of the worm stock and the migrations of the worms many points are still obscure.

Considering the statements above, the data about the influence of the ice winters on the stock of lugworms at Skallingen recorded in my earlier paper (SMIDT 1944 B) will be of no very great interest; it must be seriously considered, however, that the reduction of the *Arenicola* stock ascertained in 1942 may be due to the three severe winters of 1940, 1941, and 1942.

To find shelter from the winter cold, the worms may move deeper into the bottom. Mr. A. C. CHRISTENSEN informed me that during the cold season of the year the worms are found the whole depth of the fork down in the soil, while during the warm season they are found at only half that depth.

Pectinaria koreni MALMGREN.

1) Larval development.—The different larval stages that have been taken in plankton samples off the harbour of Esbjerg agree well with those described and figured by WATSON (1928), WILSON (1936), and THORSON (1946). The youngest stage is a *Trochophora* with an apical tuft of cilia and with many dark pigment spots all over the body. Then follows (fig. 29 A) a *Nectochaeta* stage with a prototroch and a telotroch, internal paleae, and dark pigment spots over the whole body. On the segmented part of the body these pigment spots are arranged in transverse rows. The last actually pelagic stage (fig. 29 B) has external paleae and has secreted a tube of a polygonal structure. This stage, also, has dark pigment spots on the body, arranged in transverse rows on the individual segments, and in addition some dark pigment is found

on the head. The youngest bottom stage (fig. 29 C) to be met with in the plankton, being whirled up from the bottom into the free water masses, continues the larval tube with a sand-incrusted tube. At this stage the dark pigment is limited to a spot at the base of each parapodium. All

the stages are provided with a pair of dark eye spots. These larval stages were found in small numbers in samples taken in May, June, July, and August, and the majority of them were taken in high-water samples, so it may be assumed that the main quantity is carried in from the North Sea or from the outer part of the Waddensea. The largest number of larvae was 64 per m^3 of water in a high-water sample taken in July 1942.

2) Quantitative occurrence.

—The adult bottom stages, which were taken in several places in shallow water in channels besides a single time in 1942 on the outer wadden at Skallingen, are rather scarce, their density being from 10 to 20 per m^2 . But since they occur in abundance in the shallow water along the west side of Skallingen and the islands, they must be considered to be of importance as food for the brood in the boundary area between the Waddensea and the actual North Sea.

GASTROPODA.

Hydrobia ulvae PENN.

1) Eggs and larvae. — Egg capsules surrounded by sand grains are deposited on shells of individuals of their own species, as described by several authors (see THORSON 1946). In material from the sand wadden north of Fanø taken on $13/6$ 1948 the number of eggs in 18 capsules was found to vary between 4 and 16, the average number being 10, which is in good agreement with the values found by LINKE (1939) in Jadebusen, where the number of eggs per capsule varied

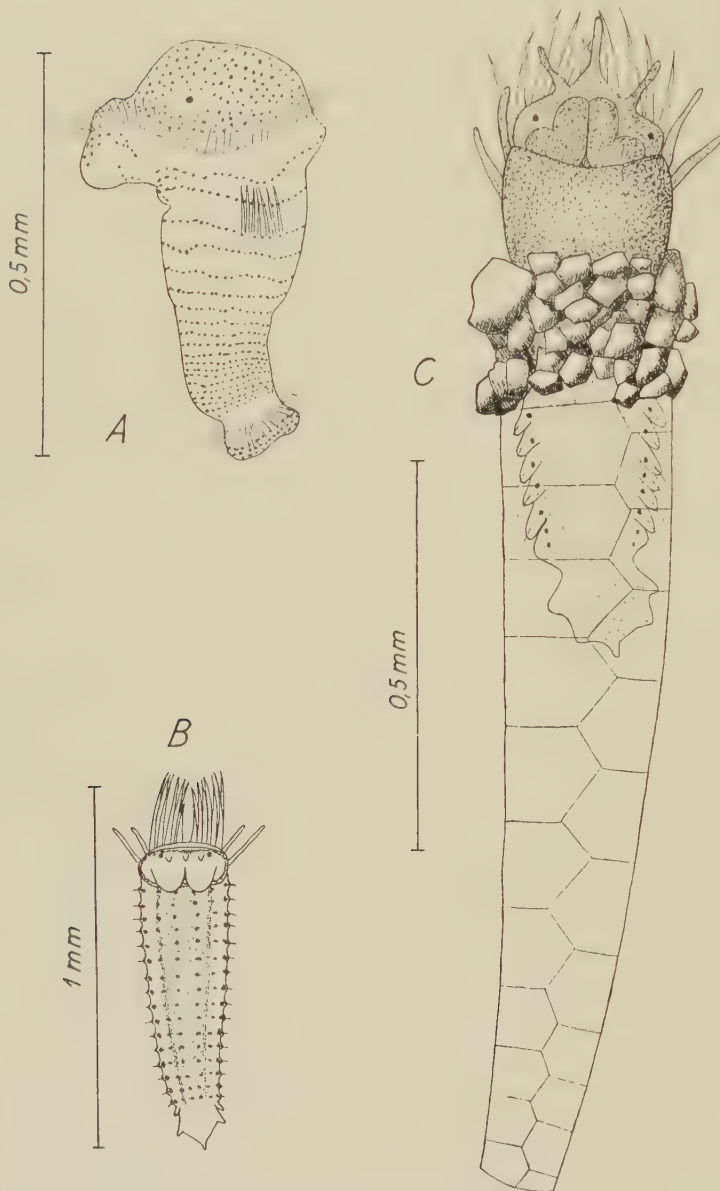


Fig. 29. *Pectinaria koreni*. A. Young planktonic larva which has not yet produced a tube (drawn from preserved specimen). — B. Older larva removed from its tube (drawn from life). — A and B from high-water plankton taken off Esbjerg on $2/7$ 1942. — C. Youngest bottom stage in the larval tube, which is continued by the permanent tube of sand grains (whirled up in the water off Esbjerg, $21/7$ 1942, drawn from life).

between 5 and 18, averaging 11. The values found by HENKING (1894) and LEBOUR (1937) likewise approximate those from the Waddensea. Egg capsules were found in the Waddensea from late in March to late in December, but the main spawning takes place in April–May, at which time over 80 per cent. of the shells may carry egg capsules (see fig. 30) and the number of egg capsules per shell may vary between 1 and 12 or more. LINKE (l. c.) reports from Jadebusen that up to 92 per cent of the shells may be covered with egg capsules, and that the number of capsules per shell ranges between 1 and 22, with an average of 4. If on the basis of observations made north of Fano, we assume that ca. 80 per cent of the shells will be beset with egg capsules, and that, on an average, 10 capsules each containing 10 eggs are deposited on each shell, it means that in a stock of 100 individuals 8000 eggs will be laid, or each pair of parents will deposit 160 eggs.

The larvae found in the egg capsules resemble those figured by HENKING (l. c.) and THORSON (l. c.). Pelagic larvae were not observed in the plankton samples, so it must be assumed that the pelagic stage is much shortened, which is in agreement with the conditions in other regions. Thus an abundant stock of *Hydrobia ulvae* is found in the harbour of Copenhagen, but no pelagic larval stage was observed during plankton investigations carried on regularly for two years (SMIDT 1944 A); and in the Sound, where the species is also abundant, a single newly hatched larva has only once been found in the plankton (THORSON 1946). The record by LINKE (1939, p. 295) of larvae found in the plankton in Jadebusen as early as the latter half of May is probably due to a confusion with larvae of *Littorina littorea*, which abound in the plankton precisely at this time of the year. That such a confusion may have taken place, is rendered probable by the circumstance that an old larva figured by HENKING (1894) and referred by him to *Hydrobia ulvae* is considered by THORSON (1946, p. 185) to be *Littorina littorea*.

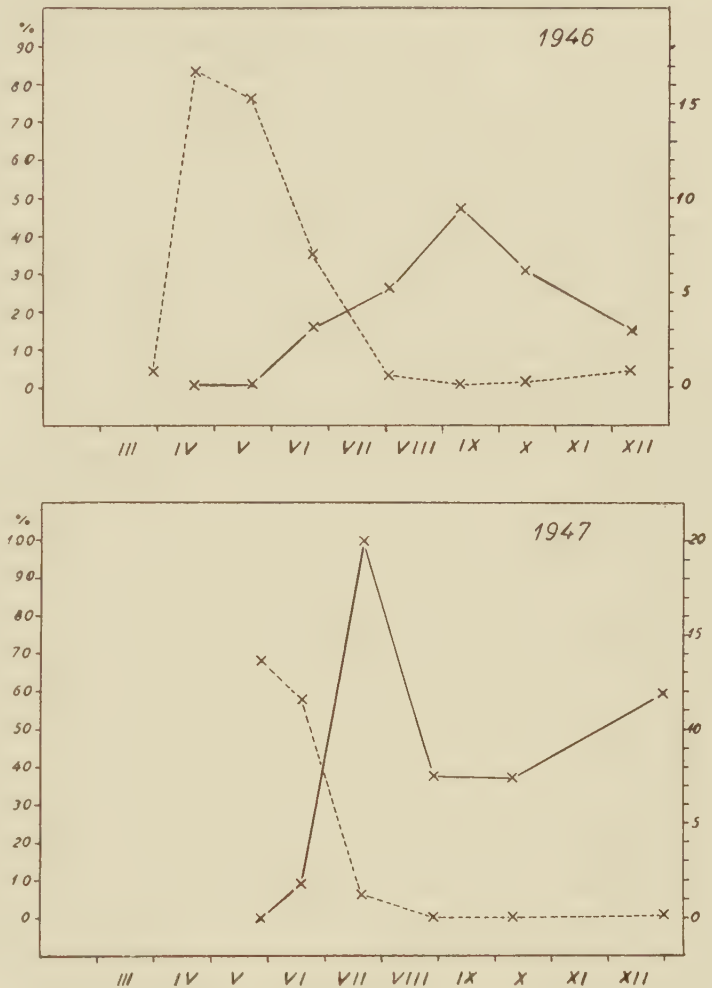


Fig. 30. *Hydrobia ulvae*. The curves show the quantity of egg capsules and the number of 0-group individuals per cm² on the wadden north of Fano in 1946 and 1947. (The broken curves indicate the percentage of adult individuals beset with egg capsules (ordinate axis, left) and the continuous curves indicate the average number of 0-group individuals per cm² in a transverse section of the wadden (ordinate axis, right).

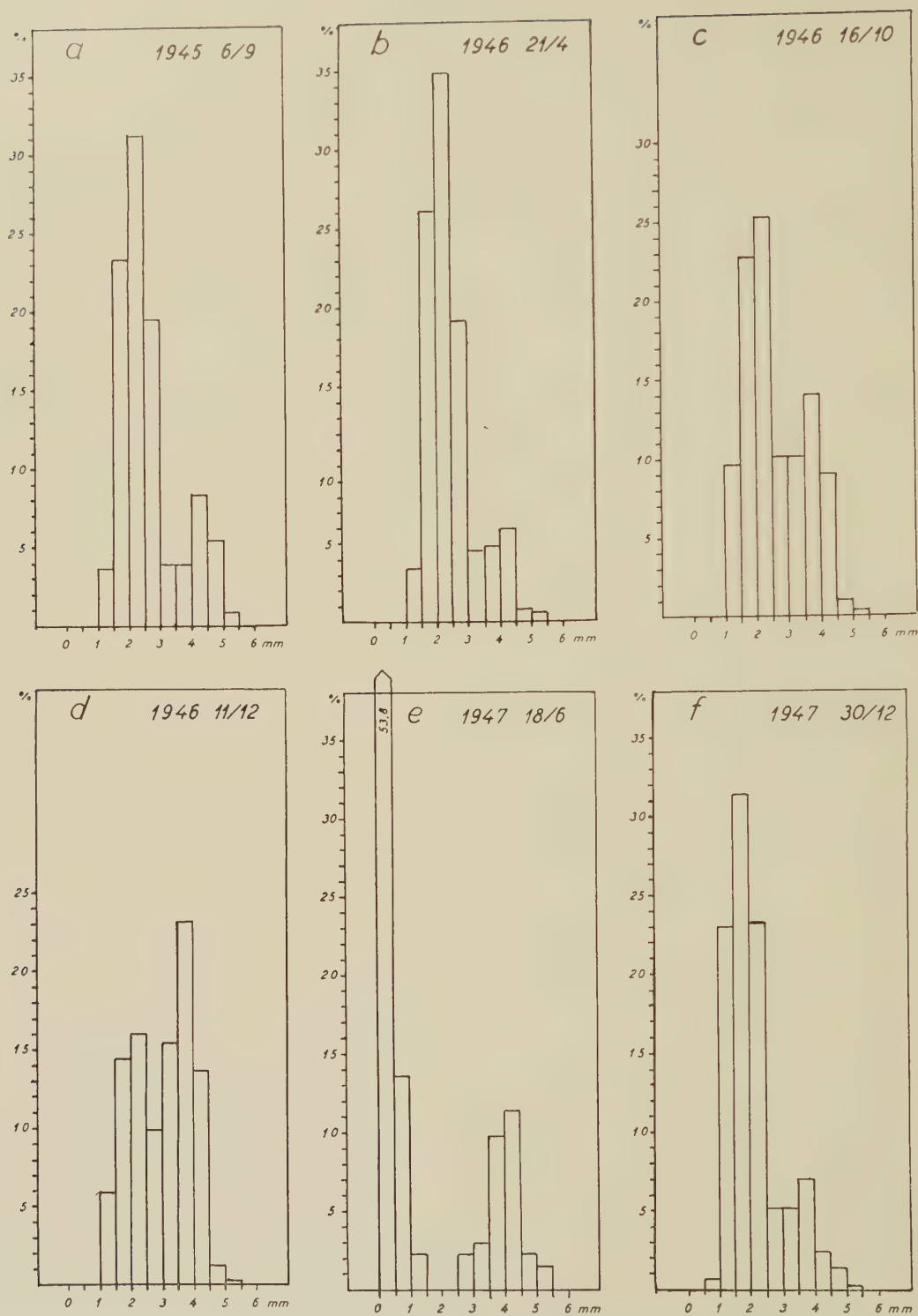


Fig. 31. *Hydrobia ulvae*. Results of measurements of shell heights of the populations on the wadden north of Fanø near the high-water mark. Of the two peaks in the diagrams, that to the left represents the 0-group, that to the right the I-group, the limiting date between the age-groups being fixed at June 1st. (Interval of measurement $\frac{1}{2}$ mm).

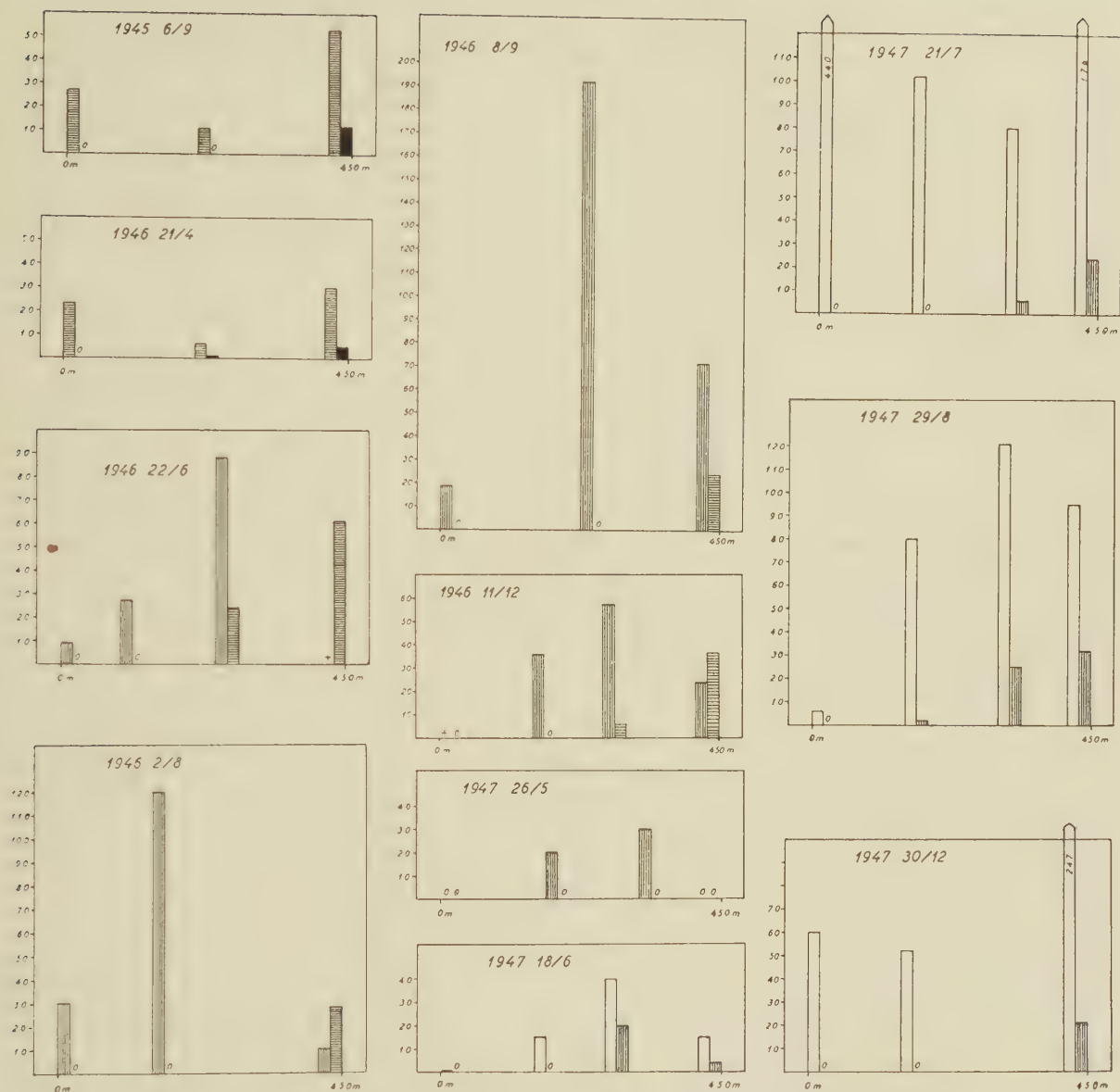


Fig. 32. *Hydrobia ulvae*. The diagrams give the numbers of individuals per m² at different times in a transverse section of the wadden north of Fano, 0 m indicating the low-water mark and 450 m the high-water mark. For each station the 0-group is indicated to the left and the I-group to the right. Black columns indicate year-group 1944, horizontally ruled columns year-group 1945, vertically ruled columns year-group 1946, and white columns year-group 1947; a + indicates that only a few animals were found in the samples, and a 0 that none were found.

The progress of reproduction in 1946 and 1947 is illustrated by the curves in fig. 30, which show the percentage quantity of adult animals beset with egg capsules at different dates on the wadden north of Fanø, and, further, the average quantity of settled animals per m² in a cross-section of the wadden.

2) Dispersal and growth.—The short-lived pelagic larval stage will probably be sufficient to enable the larvae to spread over the wadden. But a certain dispersal also takes place in that newly settled young are transported by the tidal current. The author has repeatedly, when the sea over the wadden was agitated, observed young *Hydrobia* which had been whirled up together with the rest of the microfauna. A special mode of spreading is mentioned by LINKE (1939): when young *Hydrobia* withdraw into their shells at ebb-tide, the cavity left empty will be filled with air and thus act as a float when the flood-tide sets in.

The growth is illustrated by the diagrams in fig. 31, which show the result of measurements of material collected on the wadden north of Fanø near the shore in 1945–47. Following numbers of individuals have been measured: $\frac{6}{9}$ 1945 (615 individuals), $\frac{21}{4}$ 1946 (356), $\frac{16}{10}$ 1946 (278), $\frac{11}{12}$ 1946 (375), $\frac{18}{6}$ 1947 (132), $\frac{30}{12}$ 1947 (287). The diagrams, which indicate the heights of the shells in half millimetres, distinctly show two peaks, one of which represents the 0-group, the other the older age-groups, predominantly the I-group. It will be seen that in the course of its first season the 0-group grows to an average length of about 2 mm, after which follows a winter stagnation. The succeeding season the animals, as I-group, reached an average length of about 4 mm. Considering the quantitative relation between the 0-group and the I-group (the limiting date between these was fixed at June 1st), it seems evident that only a negligible part of the stock has a possibility of sustaining life for more than the first one and a half years.

Measurements of the growth carried out by ROTHCHILD (1941) in the saltings of the river Tamar near Plymouth gave another picture than the investigations in the Waddensea, the life cycle being found to be as follows: After a spawning in the autumn, in February small individuals were found, ranging in size between 1½ and 1¾ mm. In the course of the following season the age-group grew to about 6 mm (maximum growth in April–July), those infected with *Trematodes* might attain dimensions of 9–10 mm. From the age of 17 months the population gradually died off.

3) Quantitative occurrence.—THAMDRUP (1935) found that at Skallingen *Hydrobia* is most abundant in the inner zone of the wadden; this was confirmed by my observations in other localities as far as the older animals are concerned, while the young are dispersed in large numbers all over the wadden area. The diagrams in fig. 32 illustrate the conditions prevailing on the sand wadden north of Fanø from September 1945 to December 1947. It will be seen that in the summer the 0-group is present in large numbers all over the wadden, but that a remarkable reduction takes place in the course of the year. Even the next two springs the 0-group was abundantly represented over a large part of the wadden, but then it disappeared on the outer and middle parts, so that, after passing into the I-group, it was limited to the inner wadden zone. Simultaneously with its disappearance from the outer part of the wadden, the stock, by active immigration, concentrated nearest the shore, as will especially appear from the diagrams for 1947. In that year no living animals were found in the inner zone in spring owing to the previous severe winter, but in the course of the succeeding months an immigration took place from outside, so that the stock increased gradually in number.

0-group individuals may occur on the waddens in very large numbers, while they are, as a rule, sparsely present in the channels. However, a single time (September 1945) 320,000 individuals per m² were found in a channel in shallow water at a fishing station southeast of Rømø. The occurrences may vary considerably from year to year. Thus 1946 and 1947 were years with rich broods, while 1948 and 1949 were poor breeding years. In 1946 the largest number of individuals per m² on the wadden north of Fanø was 192,000 (Sept. 8), and on the soft wadden at Fanø 663,000 were found on June 23, which is the largest number of 0-group individuals that has been found in the Waddensea so far. In 1947 the maximum number occurring on the sand wadden north of Fanø was 440,000 individuals per m² (July 21), and on the soft wadden at Nordby 640,000 per m² were found on June 22. In the channels in the northern Waddensea, on $^{20}/_6$ — $^{23}/_6$ of the same year, the 0-group was represented by a number ranging between ca. 8000 and ca. 13,000 per m². In 1948 the largest number on the wadden north of Fanø was 76,000 per m² ($^{13}/_6$), while in the channels only about 1000 per m² were found ($^{11}/_6$ — $^{15}/_6$).

The older stages (I-group and older individuals) are especially concentrated near the shore, where the largest number found on the sand wadden north of Fanø was 61,000 per m² ($^{22}/_6$ 1946). In the channels the older individuals are present in negligible numbers.

4) Mortality.—By far the greatest mortality may, no doubt, be ascribed to the action of enemies, *Hydrobia* being an important food element of many animals (fish, birds, etc.). That LINKE (1939, p. 299) mentions *Retusa truncatula* as one of the enemies of *Hydrobia*, is, according to HENNING LEMCHE (verbal information), probably due to a confusion with *Retusa obtusa*.

The effect of severe winters would seem to be limited (SMIDT 1944 B), but, as mentioned above, that part of the stock on the wadden north of Fanø which was found nearest the shore was exterminated in the ice-winter of 1947, while on the remaining part of the wadden the stock seemed to be uninjured.

An idea of the death rate among the young is obtained by considering the animals of age-groups 1946 and 1947. Roughly we may estimate the number of *Hydrobia* per m² on the sand wadden north of Fanø at 65,000 in April 1946, which according to the calculations in (1) means that the number of eggs per m² must have been 5,200,000. At the beginning of September the maximum number of young averaged 90,000 per m², that is to say that at this time the existing quantity of young corresponded to between 1 and 2 per cent. of the eggs laid, and as it must be assumed that a very considerable part of the young is consumed in the months of July and August, at the same time as settling takes place, it means that a much larger number of the eggs have reached the youngest bottom stage. Considering the conditions in 1947, we shall find that in May the average number of *Hydrobia* per m² on the wadden north of Fanø was between 10,000 and 15,000, and if we assume that their egg production in April was similar to that of the stock in 1946, the number of eggs per m² will be approximately 1,200,000 per m². The largest quantity of newly settled young, 200,000 per m² on an average, was found in July, which means that a little over 20 per cent. of the eggs shed have reached the bottom stage. Now, however, the basis of these calculations is beset with considerable errors, but as a minimum it will be safe to assume that 10 per cent. of the eggs reach the youngest bottom stage, which is a very substantial proportion compared, for instance, with the Lamellibranchs (cf. the summary below); this can be explained by the fact that the pelagic larval stage of *Hydrobia ulvae* is much shortened.

An idea of the reduction during the further growth is obtained by considering the animals from the year 1946. In September 1946 the average number per m^2 was 90,000, in December it was a little over 30 per cent. of that number (ca. 29,000 per m^2), in May 1947 hardly 15 per cent. were left, and in December 1947 only between 5 and 10 per cent. were alive. A similar reduction was ascertained for the I-group animals from the year 1945.

Littorina littorea L.

1) Eggs and larvae.—The egg capsules and the larvae, both of which are pelagic, have been described and figured by various authors (see THORSON 1946). Egg capsules were taken in plankton samples collected off the harbour of Esbjerg in the period January–September with a frequency maximum in March–June. They were almost just as common in high-water samples as in low-water samples (but several may have been overlooked in the latter). The maximum figures for the different years were (number per m^3 of water): 95 ($1^6/5$ 1942, low-water), 83 ($2^0/4$ 1943, low-water), 319 ($1^4/5$ 1944, high-water), 68 ($1^5/5$ 1946, low-water) 245 ($2^2/5$ 1947, low-water). These figures show that May was generally the month in which the most abundant spawning took place. Larvae were taken in plankton samples in the period February–December, but in large numbers only in the period May–August, and then in much larger numbers than the egg capsules. The counts revealed that 76 per cent. of the larvae were found in the low-water plankton, which shows that the maximum production takes place in the Waddensea. The largest numbers found per m^3 of water for the different years were as follows: 3,925 ($6/6$ 1942, high-water), 785 ($2^0/5$ 1943, low-water), 565 ($1^2/7$ 1944, low-water), 3610 ($2^0/5$ 1946, low-water), 6850 ($2^8/5$ 1947, low-water), which shows that the larva of *Littorina* is one of the commonest bottom animal larvae.

2) Settling and growth.—The youngest bottom stages are frequently met with as early as the end of June, attached to a fixed substratum (*Zostera* leaves and stones). It is not till later in the summer that they leave their substratum to migrate over the wadden bottom (on soft bottom, however, they chiefly seek out fixed objects).

Growth is rapid during the first two years, as shown in fig. 33 (above) for the age-group of 1946 on the wadden north of Fanø. As 0-group it grew from 4.7 mm (shell height) to 7.7 mm in the period $1^0/8$ – $1^5/10$. After a winter stagnation, the growth continued in 1947, the average height increasing from 8.2 to 12.0 mm in the period $2^0/5$ – $1^0/10$. Fig. 33 (below) shows the result of the measurement of material collected on the wadden north of Fanø on $1^0/10$ 1947. The diagram shows a clear distinction between the 0-group and the I-group, and in addition a group of older individuals is sparsely represented. The material reveals no actual numerical proportion between the groups, the 0-group being under-represented. Even greater shell heights than those measured here may occur, for in material from other wadden areas shells of a height of between 23 and 24 mm have occasionally been measured. Growth measurements of *Littorina littorea* near Plymouth (MOORE 1937) show the same growth rate for the 0-group as in the Waddensea, while in its second season the growth rate is a good deal higher near Plymouth.

3) Quantitative occurrence.—As the 0-group is densely concentrated on fixed substrata, but is otherwise of very scattered occurrence on the waddens, it is impossible to give

exact data as to its quantitative occurrence. The older individuals occur in a number of places scattered over the wadden bottom, even though some are still found congregated on fixed substrata. The density on the wadden bottom is usually low, more than some few individuals per m^2 being rarely found, and only quite exceptionally does the density exceed 50 individuals per m^2 .

4) Mortality.—Although no figures can be given for it, there is, of course, a enormous mortality among the larvae, whose pelagic life is of fairly long duration (ca. one month, cf. THORSON 1946). Nor is it possible to indicate the death rate for those living on the bottom, but no doubt a considerable reduction takes place, especially of the 0-group, owing to enemy activity. Severe winters do not seem to have any great destructive effect. In the investigations made by MOORE (1937) at Plymouth it was shown that the death rate is highest for the young, especially during their first two months, after which it steadily decreases. This is undoubtedly due to the circumstance that the young animals constitute a much more coveted prey than the older ones.

LAMELLIBRANCHIA

Cardium edule L.

1) Larval development.—Identifiable larvae like those described and figured by BARKER JØRGENSEN (1946) were only taken once in large numbers in the Waddensea, 465 larvae per m^3 of water being found in a high-water plankton-sample collected off the harbour of Esbjerg on $6/6$ 1942. On all other occasions they were sparsely present in the samples. They were taken in May–October in both high-water and low-water plankton. Everything suggests

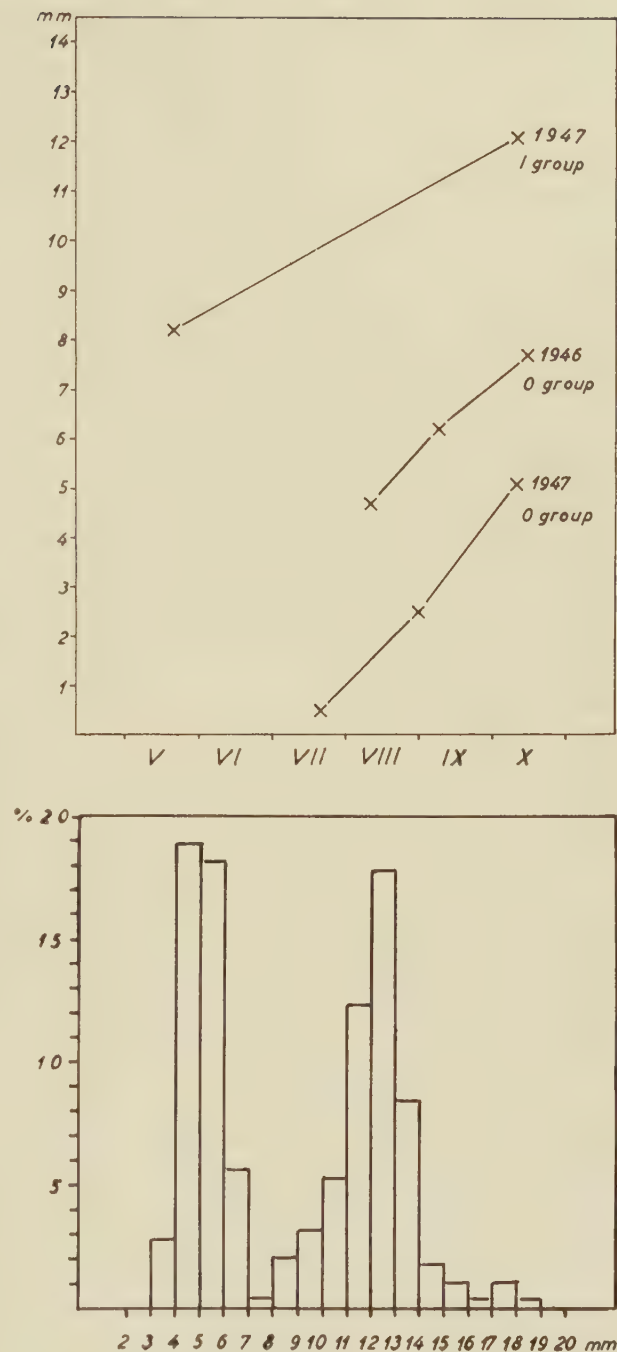


Fig. 33. *Littorina littorea*. Measurements of material from the wadden north of Fanø (interval of measurement 1 mm).—Above: Growth curves for the 0-group in 1946 and 1947 and the I-group in 1947. — Below: Material (281 individuals) collected on $10/10$ 1947; the peak to the left indicates the 0-group, that to the right the I-group.

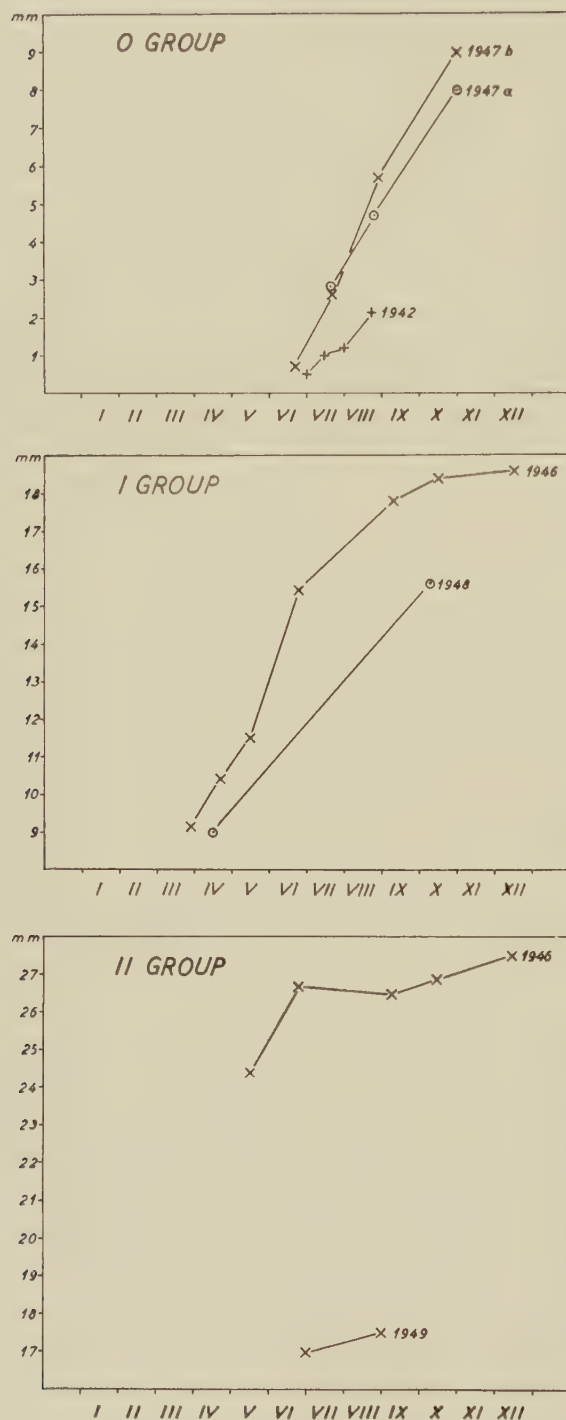


Fig. 34. *Cardium edule*. Growth curves for the 0-, the I-, and the II-group in various years on the sand waddens near Fanø. The 0-group for 1942 and 1947 a are from the wadden northeast of Fanø, all the others are from the wadden north of Fanø.

that the larvae have their maximum occurrence at the end of May and the beginning of June. Thus at this time of the year a maximum of small indeterminable Lamellibranch larvae is to be met with, and in the immediately following time (middle and end of June) the largest numbers of newly settled *Cardium* are present in microfauna bottom samples from the waddens, while microfauna bottom samples taken shortly before contained no newly settled specimens. The causes of the negligible numbers of identifiable larvae present as compared with the numbers of small indeterminable ones will be discussed in the summary (p. 91).

2) Settling.—The sparse occurrence of big pelagic larvae cannot be due to the fact that the majority settle at an early stage, for the newly settled larvae have a big prodissoconch (larval shell). By measurement of the prodissoconch of 61 newly settled individuals collected on the sand wadden northeast of Fanø on $22/6$ and $20/7$ 1947 an average length of 281μ and a variation in length ranging between 240μ and 325μ were found. These measurements come near to the largest of those found by BARKER JØRGENSEN (1946), which ranged between ca. 275 and 345μ (at Kristineberg on the Swedish coast of the Kattegat). The lowest measurements (150 — 240μ) were found by BARKER JØRGENSEN (l. c.) in the Christianshavn moat (Copenhagen), where the salinity is inconsiderable.

3) Growth.—By measurement of the shell length in material collected at different times of the year and in various localities a number of data concerning the growth were secured. The figures given here are the average figures for each sampling, and n indicates the number of individuals measured. The individual year-groups are measured apart, having been sorted by counting their winter rings (method employed by ORTON 1926, STEPHEN 1931 and 1932, and THAMDRUP 1935).

The growth conditions for the 0-, I-, and II-groups will appear from fig. 34, which is

based on the following numbers of individuals measured: 0-group 1942: $\frac{30}{6}$ (28 individuals), $\frac{16}{7}$ (275), $\frac{31}{7}$ (87), $\frac{21}{8}$ (134); 0-group 1947 a: $\frac{22}{6}$ (94), $\frac{20}{7}$ (115), $\frac{28}{8}$ (390), $\frac{30}{10}$ (55); 0-group 1947 b: $\frac{21-22}{7}$ (46), $\frac{29}{8}$ (45), $\frac{30}{10}$ (73); I-group 1946: $\frac{27}{3}$ (66), $\frac{21}{4}$ (51), $\frac{16}{5}$ (77), $\frac{24}{6}$ (75), $\frac{10}{9}$ (80), $\frac{15-16}{10}$ (114), $\frac{12}{12}$ (82); I-group 1948: $\frac{15}{4}$ (114), $\frac{10}{10}$ (77); II-group 1946: $\frac{16}{5}$ (22), $\frac{24}{6}$ (35), $\frac{10}{9}$ (32), $\frac{15+16}{10}$ (34), $\frac{12}{12}$ (29); II-group 1949: $\frac{1}{7}$ (43), $\frac{1}{9}$ (48).

It will be seen that the growth rate is highest in the first and the second summer, after which growth proceeds much more slowly. It is likewise highest in the spring and summer, decreasing in the late autumn, and being practically arrested in winter. These growth conditions agree with those found by THAMDRUP (1935) and WOHLBERG (1937) for the same sea area. It will also be seen that the growth rate is different in the various years; thus the 0-group in 1942 grew much more slowly than the 0-group in 1947. As I-group the 1947-individuals exhibited a very slow growth, as will appear from a comparison with the 1945-individuals as I-group.

There seem to be no essential differences in the growth rates between stocks on different kinds of bottom; but, as shown by both THAMDRUP (1935, pp. 74—77) and KREGER (1940), and as appears from my growth measurements, the growth rate on the waddens is the higher the longer the period of submersion is. On the sand wadden north of Fanø on June 24 and 26, 1946, some samples of 1944-individuals and 1945-individuals were taken for measurement at a number of stations from the edge of the wadden towards the shore. In these the following average length measurements were found (in mm):

Metres from the low-water mark:	ca. 10	ca. 80	ca. 170	ca. 240
1944-individuals	30.4 (n-13)	29.1 (n-11)	26.3 (n-35)	25.2 (n-3)
1945-individuals	19.0 (n-11)	17.3 (n-32)	15.4 (n-75)	14.4 (n-11)

This tendency seems to persist when we pass from the waddens into the channels, as shown by the subjoined measurements; these were made on October 30 and 31, 1947, on 0-group individuals from various sand wadden localities and various localities in the channel in Ho Bay from the outlet of the river Varde Aa to the southernmost point of Langli Sand:

Sand waddens:	Channels:
At the mouth of Varde Aa 8.5 mm (n-41)	St. a, off Varde Aa..... 9.3 mm (n-57)
Langli Sand..... 9.4 mm (n-109)	St. b, off Varde Aa..... 10.6 mm (n-168)
Northeast of Fanø 9.0 mm (n-55)	St. c, off Ho 14.6 mm (n-168)
North of Fanø..... 8.0 mm (n-73)	St. d, off Langli Sand 10.8 mm (n-165)

These values display a more rapid growth in the channels than on the waddens, as well as a decrease in size in the channel towards the mouth of Varde Aa, where the salinity is lower. THAMDRUP (l. c. p. 77) is of opinion that the cause of the increase in growth with the longer period of submersion is that *Cardium* is a suspension feeder.

4) Quantitative occurrence.—Individuals of the 0-group often occur in very large quantities, but there is a great variation in the numbers from place to place and from year to year. The largest number hitherto ascertained in any locality in the Waddensea was

found by THAMDRUP (published by SMIDT 1944 B) on Langli Sand, where almost 100,000 individuals per m² were found at a single station. Otherwise the numbers often range between 20,000 and 30,000 per m², and in many cases they are considerably lower. Already the same summer these large numbers of newly settled young are very greatly reduced, as shown by WOHLBERG (1937, p. 41) in a wadden locality at Sylt, where in the course of 1934 the following numbers of 0-group individuals were found per m²: July 39,460, August 14,000, December 4,300. That is to say that at the beginning of the winter only about 10 per cent. of the settled young were left. Some observations from the northern part of the Waddensea will further illustrate the variations in the occurrence of the 0-group:

1942 was a good breeding year, but the numerously represented 0-group disappeared almost totally before the onset of winter, and the succeeding years no representatives of that year-group were found. On the sand wadden at Skallingen 71,750 individuals per m² were found in a single locality in August, and in the same month 21,700 individuals per m² were found on a sand wadden near Sædding north of Esbjerg. On the sand wadden northeast of Fanø the following numbers per m² were registered in the course of the season: $7/6$: few individuals, $30/6$: 3,860, $16/7$: 27,500, $31/7$: 8,700, $21/8$: 13,400, $6/10$: 1,000, $24/11$: less than 1,000. On the soft wadden at Nordby (Fanø) the following numbers per m² were found in the course of the season: $30/6$: 6,000, $16/7$: 1,500, $31/7$: 3,500, $21/8$: 4,500, $4/10$: few individuals, $24/11$: 2,800. Altogether these figures show a distinct reduction in the numbers of individuals, which, however, may at times be interrupted by temporary increases (thus on the soft wadden at Nordby), due to the fact that fresh settlings of larvae are constantly taking place simultaneously with the reduction.

Unlike 1942, 1943 was a poor breeding year. On the sand wadden northeast of Fanø, 3,000 individuals per m² were found on $22/6$, and on the $20/7$ none. On the soft wadden near Nordby only a very few individuals were present on the same dates.

1946 was a fairly good breeding year; thus, on the $22/6$ 22,000 individuals per m² were found on the sand wadden north of Fanø, ca. 120 m from the low-water mark, but as early as August 2 the number had declined to less than 1,000 per m².

In 1947 no great spatfall took place, but since mortality was low, the 0-group individuals were fairly numerous at the beginning of the winter, and during the succeeding years the 1947 group played a rather important part. On the sand wadden north of Fanø, ca. 160 m from the low-water mark, the following numbers per m² were found: $18/6$: 2,200, $21/7$: 2,000, $10/10$: ca. 1,100, $30/10$: 850. On the sand wadden northeast of Fanø the figures were as follows: $22/6$: 6,100, $20/7$: 7,700, $28/8$: 4,200, $30/10$: 550. On the soft wadden at Nordby the following numbers were found: $22/6$: 16,500, $20/7$: 7,400, $28/8$: 5,200, $30/10$: 0.

In 1948 abundant settling took place, but owing to the great mortality during the season, few individuals survived till the autumn. On the sand wadden north of Fanø, ca. 160 m from the low-water mark, the following numbers per m² were found: $13/6$: 28,000, $8/7$: 11,600, $27/8$: ca. 2,700, $10/10$: few individuals.

1949 was a very poor breeding year. On the sand wadden north of Fanø ca. 160 m from the low-water mark, less than 1,000 per m² occurred on $1/7$, and at a sampling on $1/9$ only very few individuals were found.

Investigations of the quantity of young in a cross section of the wadden showed that it is lowest on the inner part of the wadden (nearest the shore) and highest on the outer one-third with the exception of the extreme outer zone. The quantities of young are as a rule much smaller in the channels than on the densely populated parts of the waddens. An example will

illustrate this: At a number of stations on the sand wadden north of Fanø, from the shore out to the low-water mark, and at four stations in channels, the number of young per m² on ²⁰⁻²¹/₆ 1946 was as follows:

	Sand wadden north of Fanø.				Channels.
Metres from the low-water mark:	ca. 5—10	ca. 130	ca. 300	ca. 440	
Numbers pr. m ² :	7,000	22,000	2,500	0	1,200—2,200

KREGER (1940), who found a similar distribution of the young according to levels, is of opinion that owing to the shorter period of submersion in the higher-lying areas a smaller number of pelagic larvae will have a possibility of settling. Whether the sparse occurrence in the shallow-watered parts of the channels is due to less settling or to a more intense persecution by enemies, it is impossible to decide. It is noteworthy, however, that in 1947, when the reduction of the 0-group was slight, a rich stock was found at several channel stations on ³¹/₁₀. Thus in the interior of Ho Bay, in a locality near the outfall of the river Varde Aa, 275 individuals per m² were ascertained, and in a locality a little farther outwards 920 individuals per m²; further, in a locality off the southern part of Langli Sand there occurred 880 individuals per m². These figures are of the same order of magnitude as those ascertained on a number of waddens: at the mouth of Varde Aa 200 per m², on Langli Sand 540 per m², northeast of Fanø 550 per m², north of Fanø 850 per m². As mentioned above, the activity of enemies was comparatively slight that year, so there is every reason to assume that an essential cause of the small number of 0-group individuals otherwise met with in shallow water in the channels is the abundance of enemies. It is very probable, however, that in deep water in channels it is the slight effect of the substratum which is responsible for the scarcity of 0-group individuals (cf. the summary on p. 92).

While the 0-group varies greatly in number from year to year, according to the larger or smaller degree of settling or the larger or smaller mortality among the young, the older stock will remain more stable from year to year, provided that no remarkable catastrophes set in (e. g. severe winters). In most cases it seems to be a single or some few years' production which dominates the population for several years, as was shown by THAMDRUP (1935). As a supplementary example it may be mentioned that the 1947-individuals were sole dominants on the sand wadden north of Fanø in 1948 and 1949. In other places, also, it has been demonstrated that it is certain age-groups which dominate for a number of years, thus at the Scotch coast (STEPHEN 1931 and 1932).

THAMDRUP (l. c.) showed that the adult stock has its maximum density on the outer half of the wadden, and a similar distribution was revealed by my observations. As an example the numbers per m² found on the sand wadden north of Fanø in June 1946 will be given (the 1945-individuals constitute about 70 per cent.):

Metres from the low-water mark	ca. 10	ca. 80	ca. 170	ca. 240	ca. 320	ca. 430
Numbers per m ²	few	430	504	180	90	0

While the 0-group may be numerously represented in all localities, the older age-groups were only found to be abundant on sand waddens, whereas they exhibit little density on soft waddens and in channels.

5) Mortality.—From the above it will appear that the death-rate among larvae and the youngest bottom stages is very high, while among the older age-groups it is normally low. It turned out that the 1947 year-group was not much reduced in the years 1948 and 1949. On the other hand, exceptionally severe winters may totally exterminate a whole stock (cf. SMIDT 1944 B). An especially striking instance of this was the effect of the severe winter of 1946—47, which entirely killed off the 1945-individuals, which were numerous on the waddens at Fano in 1946, so that in 1947 the waddens were strewn with empty shells.

Macoma baltica L.

1) Larval development.—The veliger, which is described and figured by WERNER (1939) and BARKER JØRGENSEN (1946), was found in plankton samples taken off the harbour of Esbjerg in April—October. The majority (ca. 60 per cent.) of the larvae counted were taken in high-water samples. It is possible, however, that some of the larvae noted down as *Macoma* belong to other *Tellinidae*, from which they are difficult to distinguish. The identifiable larvae were present in the samples in small numbers only, but it must be assumed that a number of the small indeterminable Lamellibranch larvae belong to *Macoma*. As the maximum number of newly settled larvae is found on the waddens in June, it can be taken for granted that the main spawning takes place in May.

2) Settling and growth.—Settling takes place on all qualities of bottom mainly in May—June, but newly settled larvae may be found even in the late autumn. In June the newly settled larvae are under $\frac{1}{2}$ mm long; thus 119 individuals on the mud wadden at Nordby on $\frac{30}{6}$ 1942 exhibited an average length of 0.4 mm, and none of them was over 1 mm long. The material of 0-group individuals found in samples taken in the autumn is so sparse that it gives no reliable picture of the growth; but that the growth is slow, appears from investigations made at the Scotch coast (STEPHEN 1931), where the 0-group in the course of the first season reached an average length of 5 mm, and as I-group it attained a length of 8—9 mm at the end of the second season. The growth of the older age-groups was investigated by THAMDRUP (1935), who found that unlike *Cardium*, *Macoma* exhibits no differences in growth-rate in the different parts of the wadden. THAMDRUP (l. c.) explains this as due to the fact that *Macoma*, being a deposit feeder, in its food uptake is independent of the duration of the water-covering period.

3) Quantitative occurrence.—The 0-group is often abundantly represented on all types of wadden. The maximum number for a soft wadden (16,000 per m²) was found at Nordby on $\frac{30}{6}$ 1942, while the maximum number for a sand wadden (5,900 per m²) was found northeast of Fano on $\frac{22}{6}$ 1946. From the wadden at Skallingen THAMDRUP (1935) gives the maximum number for the 0-group as 6,325 per m². The number of newly settled individuals in the channels is considerably lower than on the waddens. The above-mentioned figures show that *Macoma* settles in much smaller numbers than *Cardium*, but like the latter, *Macoma*, too, is much reduced in number during its first season. This decline, however, may be interrupted by temporary increases of number later in the year, settling taking place during the whole season. A few examples will be mentioned: on the soft wadden at Nordby the following numbers per m² were found in 1942: $\frac{30}{6}$: 16,000, $\frac{16}{7}$: 5,000, $\frac{31}{7}$: 1,600, $\frac{21}{8}$: less than 500, $\frac{4}{10}$: 1,800, $\frac{24}{11}$: 1,200; and on the sand wadden northeast of Fano the following numbers per m² were found in 1947: $\frac{22}{6}$: 5,900, $\frac{20}{7}$: 3,500, $\frac{28}{8}$: less than 500, $\frac{9}{10}$: 0.

The older age-groups rarely occurred in any great numbers. The largest number has been found on the wadden at Skallingen, where THAMDRUP (1935) in July 1932 observed up to 1,000 per m², and in August 1942 the present author (SMIDT 1944 B) found up to ca. 700

per m². At all other samplings in the remaining part of the Waddensea more than 200 per m² have rarely been found, and in most cases less than 100 individuals per m² were secured.

4) Mortality.—The great mortality among the 0-group individuals can be ascribed to persecution by enemies. As to the older age-groups the mortality seems to be inconsiderable, and even severe winters do not seem to have any harmful effect on the stock (SMIDT 1944 B).

Scrobicularia plana L.

As to the larval development no observations are available. THAMDRUP (1935) states that fairly large quantities of young individuals were found in the summer of 1934 on a wadden area at Skallingen, and at my samplings on the soft wadden at Nordby on ³⁰/₁₀ 1947 occasional individuals of the 0-group were found.

The older age-groups are probably distributed everywhere on soft and mixed bottom, but have never been observed in any great quantities. As a maximum on the wadden at Skallingen THAMDRUP (l. c.) found 60 individuals per m² (July 1933), while only a very few were found the two previous years.

Although the older age-groups are deeply buried in the bottom, they seem to be very sensitive to severe winters (SMIDT 1944 B). As an example it may be mentioned that on the soft wadden at Nordby an abundant stock was found in 1946, but after the severe winter of 1946—47 it seemed to have entirely died off in 1947.

Mya arenaria L.

1) Larval development.—The identifiable larvae described and figured by C. BARKER JØRGENSEN (1946) were taken in plankton samples off the harbour of Esbjerg in the period May—October, and in May—August they were occasionally collected in considerable numbers. The maximum number (535 larvae per m³ of water) was taken in a low-water sample on ¹²/₇ 1944. On most sampling days more larvae were found in the water at high-tide than at low-tide. It also appears from the counts that certain years, as 1947, were especially rich in larvae, while others, for instance 1946, were poor in larvae.

2) Settling.—On settling, the larvae seem to be indifferent to the quality of the bottom, large quantities of young having been found on sandy as well as on soft waddens. In good breeding years with abundant brood the maximum settling takes place in June, but throughout the summer there is a considerable spatfall. Peculiar to the youngest bottom stage is the secretion of byssus filaments, which often combine many of the small *Mya* in a network.

3) Growth.—In the course of its first season, the brood generally attains an average length of 2—3 mm. That this is not greater, is due to the fact that fresh broods will constantly settle, so at the end of the season the smallest individuals are less than 1 mm long, while the biggest are 5—6 mm long. This will be exemplified by some figures, all from ²⁹/₈ 1947: on the soft wadden at Nordby 169 individuals of the 0-group had an average length of 2.9 mm (varying between ¹/₂ and 6 mm), on the sand wadden northeast of Fanø the average length was 2 mm (varying between 1 and 5 mm), and on the sand wadden north of Fanø the following figures were found at three stations: near the low-water mark 42 individuals had an average length of 2.1 mm (varying between ¹/₂ and 5 mm), ¹/₃ of the distance towards the shore of the wadden 47 individuals had an average length of 3 mm (varying between 1 and 5 mm), and ²/₃ of the distance in on the wadden 21 individuals had an average length of 4.6 mm (varying between 3 and 6 mm).

No measurements of growth are on record for the older age-groups, but probably the growth is not very different from that found by NEWCOMBE (1933) for Canadian *Mya arenaria*, for by measuring the winter rings he arrived at the following figures: ring no. 2: 19.5 mm, no. 3: 31.3 mm, no. 4: 41.7 mm, no. 5: 49.8 mm, no. 6: 56.9 mm, no. 7: 63.0 mm.

4) Quantitative occurrence.—In some years 0-group individuals are present in great abundance, in other years in negligible numbers, and there seems to be a certain correlation between the quantity of planktonic larvae and the quantity of 0-group ^{individuals} larvae. In 1942 large numbers of settled individuals were found (e. g. on $^{30}/_6$ 20,000 per m² on the soft wadden at Nordby), and some time before ($^6/_6$) a considerable number of larvae were found in the plankton. 1946 was poor in both larvae and newly settled individuals. In 1947 large quantities (see below) settled in June, and plankton samples from May contained considerable quantities of larvae. 1948 and 1949 were very poor in newly settled individuals, but no information about the occurrence of pelagic larvae is available.

In years with abundant brood the maximum number of 0-group ^{individuals} larvae occurred in June, after which time a considerable reduction takes place; however, owing to a continued settling minor increases of the numbers may take place in the course of the summer. As an example some figures for the rich brood year of 1947, the year in which the absolutely largest numbers of newly settled animals occurred, will be given: On the soft wadden at Nordby the following numbers per m² were found: $^{22}/_6$: 43,000, $^{20}/_7$: 26,000, $^{28}/_8$: 11,600, $^{30}/_{10}$: 0. On a sand wadden area north of Fanø the numbers were as follows: $^{18}/_6$: 30,000, $^{21}/_7$: 11,800, $^{29}/_8$: 9,400, $^{30}/_{10}$: ca. 100.

Since, in general, the majority will be killed already during their first season, the quantity of older age-groups is sparse; these latter seem, however, to occur in patches. THAMDRUP (1935) found 20 per m² as a maximum number on the wadden at Skallingen, but generally much fewer are found. An exceptionally large number of individuals of the I-group were taken in 1941 in a sand wadden locality on Rejsby Stjert (line 11, fig. 40, p. 121), where at two stations situated near each other, 1000 and 1300 individuals per m² were found.

5) Mortality.—While the 0-group has a high death-rate owing to persecution by enemies, among the older age-groups it will hardly be very high under normal conditions. It would seem, however, that severe winters may have a destructive effect (SMIDT 1944 B).

Mytilus edulis L.

1) Larval development.—The larvae, which have been described and figured by several authors (cf. BARKER JØRGENSEN 1946), were most abundant in plankton samples taken off the harbour of Esbjerg in the period May—November (a single larva taken in February 1943). In good agreement with this KÄNDLER (1926) reports that the larvae occur in the plankton at Heligoland in the period April—December, and BARKER JØRGENSEN (l. c.) states that in the Sound they are found from May to December or January. By far the majority of the counted larvae (ca. 90 %) were taken in high-water samples. The richest sample (high-water sample, $^6/_6$ 1942) contained 286 larvae per m³ of water. Several of the small indeterminable Lamelli-branch larvae found should probably be referred to the *Mytilus* larvae.

2) Settling and growth.—The newly settled animals are chiefly met with on a firm substratum (stones and shells), but also on the waddens (both on sandy and on soft bottom) the youngest bottom stages may be encountered, though in negligible numbers as compared with the other Lamellibranchs.

Measurements of the growth were not carried out in the Waddensea, but in the Limfjord, where conditions hardly differ very much from those of the Waddensea, SPÄRCK (1919) found that young *Mytilus* in the course of about one month after attachment (from the end of May to June 25) attained a length of 4 mm. In Passamoquoddy Bay (Canada) WARREN (1936) showed that in the course of 28 days young *Mytilus* which were constantly covered with water reached a length of ca. 4 mm (that is, precisely the same growth as in the Limfjord), and in 56 days they attained a length of ca. 8 mm. At the same time it turned out that young *Mytilus*, which were laid bare for about four hours daily, attained a length of 1 mm in the course of 28 days, and in the course of 72 days a length of hardly 4 mm. As the *Mytilus* banks in the Waddensea lie both above and below the low-water mark, the growth conditions will probably exhibit various differences, as it may be assumed that the above-mentioned figures do not differ very much from those to be found in the Waddensea.

3) Quantitative occurrence.—While *Mytilus* is of sparse occurrence outside the banks, inside these it is present in very large numbers, THAMDRUP (1935) having calculated the numbers per m² to be between ca. 2,000 and 12,000.

4) Mortality.—Immense quantities of 0-group ^{Indiv. Decks}larvae must be assumed to be consumed by enemies. In Passamoquoddy Bay WARREN (l. c.) found that *Mytilus* is very sparingly present below the low-water mark, where its enemies (star-fish and other invertebrates, and fish) are numerous, while it thrives especially well there if protected against these enemies.—Among the older *Mytilus* there is hardly any great mortality under normal conditions, but severe winters may have a highly destructive effect, as it was possible to ascertain after the winters of 1940, 1941, and 1942 (SMIDT 1944 B) and after the winter of 1947.

CRUSTACEA.

Balanus.

Two species of *Balanus* are numerous in shallow water wherever there is a fixed substratum. The pelagic larvae (*Nauplia*) are produced in all the months of the year, but the largest numbers were found in plankton samples from March—June. The maximum figures for the different years were (number per m³ of water): 1942: 1,835 (⁶/₆, high-water), 1943: 1,600 (²¹/₅, high-water), 1944: 1,530 (¹⁹/₃, high-water), 1947: 548 (²²/₅, high-water). Of all the *Nauplia* counted, 70 per cent. were found in high-water samples, which fact will be discussed in the summary (pp. 91—92). In addition to the *Nauplia*, the plankton samples contained limited numbers of the *Cypris* stage.

As regards growth and mortality, no observations are available from the Waddensea.

Corophium volutator (PALLAS).

1) Reproduction.—According to HART (1930) the spawning time in South England is April—September, and the same is confirmed by THAMDRUP (1935) for the population of the Waddensea. HART (l. c.) states that there are several spawnings a year. The last hatched brood becomes sexually mature in winter and spawns next April, while those which become sexually mature in summer die the succeeding autumn and winter; the stock accordingly survives for half a year. THAMDRUP (l. c.) has made interesting observations on the biology of the brood: the brood, which is non-pelagic, remains during its first time in the tube of the mother animal; later the young form special tubes issuing from the mother tube, but gradually the connection with the mother tube is interrupted and they become independent tubes.

2) Quantitative occurrence.—It is stated in the literature that considerable quantitative fluctuations take place in the course of the year as well as from year to year (SEGERSTRÅLE 1927, THAMDRUP 1935). Thus THAMDRUP (l. c.) states that in the autumn of 1933 there was a particularly rapid increase in the number of individuals on the wadden at Skallingen (maximum number 7,123 per m²) as a consequence of excessive brood production in the course of the summer.

On the wadden north of Fanø quantitative investigations were made in 1946 and 1947, and both years exhibit about the same picture: a maximum in June—July, after which the

number decreased to a very low value in the autumn (see fig. 35, which illustrates the conditions nearest the shore). The maximum number in 1946 (June) was 1,300 per m², in 1947 (July) 2,170 per m².

On the soft wadden at Nordby the following numbers were found in 1947: ²⁸/₈ 3,300 per m², ⁸/₁₀ 180 per m².

Even much denser populations of about 20,000 per m² were observed in different places in the Waddensea. The greatest density was found in August 1941 off Højer, viz. 24,800 per m².

As regards changes in the populations, we should be alive to the possibility of migrations, for *Corophium* is often seen swimming when the

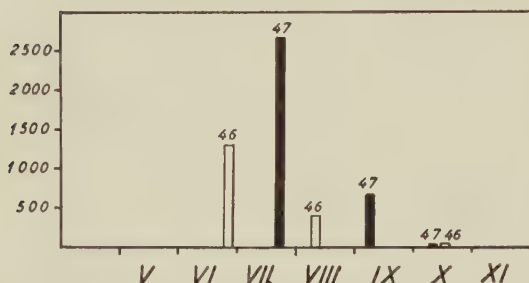


Fig. 35. *Corophium volutator*. Numbers of individuals per m² on the wadden north of Fanø near the high-water mark in 1946 (white columns) and 1947 (black columns).

wadden is covered with water. BEANLAND (1940) thinks that *Corophium* often swims about, to settle finally on suitable bottom.

3) Mortality.—The heaviest mortality must be assumed to be due to persecution by enemies, *Corophium* being a favourite food animal of many invertebrates, fish, and birds. This is no doubt the explanation of the decline of the population on the wadden north of Fanø in 1946 and 1947. Ice winters do not seem to leave perceptible traces in the populations of the succeeding season (SMIDT 1944 B), i. a. the abundant population north of Fanø in 1947 followed upon a severe winter. To be sheltered from the cold, *Corophium* burrows deeper into the bottom in winter than in summer (LINKE 1939).

Mysis flexuosa O. F. MÜLLER.

The species, which may be abundant in the channels, at ebb-tide is only found scattered on the waddens in pools. The young, in a few specimens, were observed in plankton samples taken off the harbour of Esbjerg in the months August, September, and October. According to the investigations of BLEGVAD (1921) in the inner Danish waters, the life cycle of the species is as follows: The spawning time is from the middle of May to well into October. Individuals surviving the winter die off the next summer after having spawned three times; from the eggs two generations arise, which, again, will spawn several times. *Mysis flexuosa* is pursued by many fish, as it is a valuable food element.

Crangon vulgaris FABR.

1) Reproduction and growth.—Publications on the reproduction of *Crangon vulgaris* are summarised by THORSON (1946), and since then LLOYD & YONGE (1947) have published

a comprehensive work on the biology of the species. According to the literature it has two spawning periods, one in the spring and early summer and one in the autumn and winter. Sexual maturity sets in when the species is about one year old, and it is assumed that it may reach an age of three years. In plankton samples from the Waddensea pelagic larvae were found in the period May—October, most numerous in June—July, and by far the majority were taken in high-water samples. The maximum number was 38 per m³ of water (high-water sample ¹⁴/₇ 1942).

2) Occurrence of the bottom stages.—The youngest bottom stages are frequently found in summer and autumn on the waddens (up to a little over 100 per m²). The older stages, however, are only exceptionally met with on the waddens—at any rate at ebb-tide—whereas they are numerous in the channels, where they were taken with the young plaice trawl in very large quantities in summer and autumn. According to the available literature, they migrate from the shore out to deeper water in winter (EHRENBAUM 1890, HAVINGA 1929, MEYER 1935, LLOYD & YONGE 1947).

3) Mortality.—As *Crangon* is an exceedingly important food element for many animals, it must be assumed that a substantial part of the population is reduced by enemies, but no quantitative data can be given.

Carcinus maenas L.

A survey of the literature on the reproduction of the species is found in the paper of THORSON (1946). In most places spawning seems to occur all the year round, but at certain times of the year—differing somewhat in the various places—spawning is especially abundant. In the Waddensea rather few *Zoea* were found in plankton samples in the period May—September (maximum number in June—July), and by far the greater number were taken in high-water samples. The maximum of *Zoea* found was 11 per m³ of water (¹⁴/₇ 1942) in a high-water sample. Some few *Megalopa* were observed in July—August (1942).

The young bottom stages are frequently met with in summer (especially in August) on the waddens, though the density is not great (rarely over 100 per m²). The adults, however, which occur in great abundance in the channels, are only exceptionally encountered on the waddens at ebb-tide.

ECHINODERMA.

Asterias rubens L.

A survey of the literature on the reproduction of the species is found in the paper by THORSON (1946). The pelagic larvae were found, in the Waddensea, in plankton samples in the period March—July with a maximum in April—May. The largest number of larvae, 165 per m³ of water, were taken on ¹⁴/₅ 1944 (low-water sample). When the larvae were counted, 71 per cent. were found in the high-water samples.

In places the adults are exceedingly numerous in the channels, and in October 1949 fishing of star-fish was commenced in Ho Bay off Hjerting, the star-fish being bought by the herring oil factory and meat fodder factory at Esbjerg. But already in the summer of 1950 the stock had been practically fished up, so the fishing had to be stopped. According to information from the Danish Ministry of Fisheries, the quantities fished in the various months were as follows:

1949 October	166,000 kg	1950 March	35,000 kg
November	54,000 -	April	45,000 -
December	43,000 -	May	6,000 -
1950 January	25,000 -	June	2,000 -
February	21,000 -	July	700 -

Thus since 1949 a total of 397,700 kg of the stock off Hjerting has been fished, and assuming that a quantity of about 90 per cent of the whole population was fished up, it means that the total stock amounted to ca. 440,000 kg, as it may be taken for granted that as far as the weight is concerned, only a minimal addition of young can have taken place during that period.

B. Summary and Discussion.

1) Reproduction.—The following modes of spawning are found in the above-mentioned species: A number of species have brood protection, the eggs being protected in different ways during the embryonic development; this is the case in *Capitella capitata*, *Pygospio elegans*, *Polydora ligni*, *Balanus* sp. sp., *Corophium volutator*, *Mysis flexuosa*, *Crangon vulgaris*, *Carcinus maenas*. In the following species the eggs are shed in gelatinous masses, which are attached to a substratum: *Phyllodoce maculata*, *Scoloplos armiger*, *Hydrobia ulvae*. Pelagic egg capsules are found in *Littorina littorea*. Several species spawn their eggs freely in the water: *Eteone longa*, *Nereis diversicolor*, *Nephtys hombergi*?, *Arenicola marina*, *Heteromastus filiformis*?, *Lamellibranchia*, *Asterias rubens*.

The larval development is non-pelagic in two species, viz. *Scoloplos armiger* and *Corophium volutator*, while the other species have a pelagic development. The pelagic larvae can be referred to the three categories erected by THORSON (1946): A) Planktotrophic larvae (feeding on planktonic organisms) with a long pelagic stage are found in *Phyllodoce maculata*, *Eteone longa*, *Nephtys hombergi*, *Pygospio elegans*, *Polydora ligni*, *Capitella capitata*, *Pectinaria koreni*, the *Lamellibranchs* mentioned above, *Littorina littorea*, *Balanus* sp. sp., *Mysis flexuosa*, *Crangon vulgaris*, *Carcinus maenas* and *Asterias rubens*. B) Planktotrophic larvae with a much shortened pelagic stage are found in *Arenicola marina* and *Hydrobia ulvae*. C) Lecithotrophic larvae (feeding on their own yolk) are probably only represented by the presumed *Heteromastus filiformis* larvae. To which group *Nereis diversicolor* should be referred, is doubtful. The lecithotrophic larval type described by THORSON (l. c.) does not seem to occur in the Wadden-sea; probably the development here is entirely non-pelagic or a much shortened pelagic development, as the larvae found in the plankton must be regarded as whirled-up bottom stages.

Of the above-mentioned methods of reproduction, that with a long pelagic development is the most wasteful, a very great proportion of the brood being doomed to destruction before they reach the bottom stage. A comparison between the *Lamellibranchs* with a pelagic development and *Hydrobia ulvae* will serve to illustrate this. The brood production of the *Lamellibranchs* is enormous; thus FIELD (1911) states that he observed four *Mytilus* in the course of a quarter of an hour spawning from 6 to 12 million eggs each, and it is obvious that by far the greater part of this egg quantity will be destroyed before the bottom stage is reached. SPÄRCK (1927) assumes that of 1 million *Ostrea edulis* larvae, only one reaches the stage of attachment. In comparison the losses sustained by *Hydrobia ulvae* are inconsiderable, the

above-mentioned investigation having shown that about 10 per cent. or more of the eggs spawned may be assumed to reach the bottom stage.

On counting the bottom animal larvae occurring in the plankton samples it turned out that Spionid larvae (*Pygospio* and *Polydora*), Lamellibranch larvae, *Littorina* larvae, and *Balanus Nauplia*, that is, chiefly larvae of animals living in the tidal area, were by far the most numerous. These larvae are distributed as follows over the high- and low-water samples taken off Esbjerg (percentage for low-water samples): *Spionidae* 68, *Lamellibranchia* 25, *Littorina* 76, *Balanus Nauplia* 30.

The much greater abundance of Spionid larvae and *Littorina* larvae in the low-water than in the high-water plankton can be explained by the large production that takes place in the Waddensea.

The Lamellibranch larvae are remarkable by being comparatively few in number in the low-water samples and by consisting predominantly of small indeterminable specimens (the maximum number counted of small indeterminable Lamellibranch larvae was about 2000 per m³ of water in a high-water sample, ¹⁴/₇ 1942). The small number of identifiable *Cardium* larvae found in the samples is especially remarkable considering the large quantities of newly settled *Cardium* larvae that are met with on the waddens. These facts must probably be connected with the large quantities of Spionid larvae which occur in the low-water plankton simultaneously with the main occurrence of the Lamellibranch larvae; for the Spionid larvae no doubt devour the Lamellibranch larvae to a great extent, which explains the scarcity of big Lamellibranch larvae on the whole, and the relative scarcity of Lamellibranch of all sizes in the low-water plankton. This view is supported by the following facts: In the Sound THORSON (1946) observed that larvae of *Polydora ciliata* devour Lamellibranch larvae, and in the harbour of Copenhagen they have been seen to devour *Rotatoria*, which are of a similar size to the Lamellibranch larvae (SMIDT 1944 A). In the Mediterranean CERRUTI (1942) observed and photographed *Polydora hoplura* devouring *Ostrea* larvae. As a further illustration of the relation between *Polydora* larvae and Lamellibranch larvae some observations made by SPÄRCK (1926) will be mentioned: Water from the Limfjord containing quantities of both Lamellibranch larvae and *Polydora* larvae was transferred to some tanks. After some time nearly all the Lamellibranch larvae had disappeared, while the bottoms of the tanks were covered with tubes of Polychaetes, i. a. *Polydora ciliata*. THORSON (l. c.), on the basis of his experience from the Sound, explains this by the assumption that the *Polydora* larvae had devoured the Lamellibranch larvae. In agreement with these observations the author (SMIDT 1944 A) ascertained that in the south harbour of Copenhagen very few big Lamellibranch larvae are present, while at the same time larvae of *Polydora ciliata* are exceedingly numerous. In addition to the Spionid larvae the Lamellibranch larvae in the Waddensea have several other enemies which may limit their numbers. Of the Polychaete larvae, mention should be made of *Magelona*, which is of common occurrence in the plankton of the Waddensea, and which in great part seems to live on Lamellibranch larvae (LEBOUR 1922, THORSON l. c., observations by the author in the Waddensea). Further, both *Mytilus* and *Balanus* seem to eat a number of Lamellibranch larvae (CERRUTI 1942).

It is a peculiar fact that *Balanus Nauplia* occur much more frequently in the high-water than in the low-water plankton, though it must be assumed that the greatest production takes place in the Waddensea. The explanation may to some extent be the same as for the Lamellibranch larvae, namely that it is the activities of their enemies which reduce the number in the Waddensea, but the explanation does not seem satisfactory. Of the enemies which can be supposed to be of importance, the following may be mentioned: Young herrings, which

in summer are very common in the Waddensea, and are known to take i. a. Cirriped *Nauplia* (JESPERSEN 1928); in addition *Cirripedia* devour i. a. their own *Nauplia* (GRUVEL 1893, p. 553), and in the stomach contents of *Mytilus edulis* i. a. remains of *Cirripedia* larvae have been found (COE 1945).

A more satisfactory explanation of the under-representation of the *Balanus Nauplia* in the low-water samples, may perhaps be found in the assumption that the larval production is higher in the constantly water-filled channels than on the waddens. As the water off the harbour of Esbjerg at low-water must be assumed to be that which has receded from the southern waddens during the ebb period, the plankton will be marked thereby. That, at any rate, is the best explanation why larvae of species which as adults are abundant in the channels but few in number or rare on the waddens, are most numerous in the high-water plankton (e. g. *Crangon vulgaris*, *Carcinus maenas*, and *Asterias rubens*).

2) Settling of pelagic larvae.—As already pointed out, a very considerable settling of pelagic larvae takes place on the waddens during the summer, and this settling seems to be stimulated by the bottom material present. WILSON (1932, 1937, and 1948) and DAY & WILSON (1934) made some fine experiments with different Polychaete larvae, and these experiments show that the larvae settle rapidly when a suitable substratum is present, while an unsuitable substratum will prevent or impede settling for a long time. Further, JÄGERSTEN (1940) has demonstrated the effect of the substratum on some larvae of *Protodrilus*, and MORTENSEN (1921 and 1938) has shown it for some Echinoderm larvae. THORSON (1946) discusses the problem at length, and at the same time records some interesting observations made during experiments with the so-called "bottle-collector" in the Sound, where it turned out that various larvae belonging to widely different animal groups had settled or had attached themselves to the substratum suitable to them and only there (e. g. metamorphosed stages of *Zirphaea crispata* were found boring in the cork floats and only there, metamorphosed *Pomatoceros triqueter*, *Balanus improvisus*, *Psolus phantapus*, and *Anomia squamula* attached to the smooth glass walls and only there, and in the detritus material at the bottom of the collector various species of Prosobranchs, Lamellibranchs, Echinoderms, and Polychaetes were found). Finally COLE & KNIGHT (1949) have shown experimentally that larvae of *Ostrea edulis* L. prefer to settle on shells coated with a film of bacteria and diatoms instead of shells from which such a coating has been removed, and further, that they settled more frequently on shells to which settled young were already attached than on shells from which the young had been removed. JÄGERSTRÖM (l. c.) in his experiments with *Protodrilus* arrived at the result that settling is caused by a chemical factor, while WILSON (1948) in very careful experiments with *Ophelia* was unable to find any chemical factor, whereas it was shown that it depended on the size and shape of the sand grains whether or not the larvae metamorphosed.

My aforementioned experiments with larvae of *Pygospio* and *Polydora* from the Waddensea show that these are stimulated to settling when they are placed in glass vessels containing a natural substratum (both sand and mud), whereas settling fails to take place or is retarded in vessels to which no such bottom material has been added. Accordingly these Polychaete larvae are not much specialised in their choice of a substratum, which accords with the fact that the adult animals occur on rather diverse kinds of bottom.

At the collecting of micro bottom samples on waddens with different qualities of bottom, no preference for any particular quality of bottom was found for the Lamellibranch brood. Experiments concerning the effect of the substratum on Lamellibranch larvae were not carried out owing to a too sparse material of larvae and to technical difficulties; but since, according

to the above, the effect of the substratum seems to be a phenomenon commonly met with among widely different animal groups, and was also demonstrated for the Lamellibranchs by COLE & KNIGHT (l. c.) and THORSON (l. c.), it is highly probable that it is active also among the Lamellibranchs living on the waddens. Another circumstance speaks in favour of this assumption: Considering the small numbers of identifiable Lamellibranch larvae that are found in the plankton samples, the number of newly settled Lamellibranchs found on the waddens is astoundingly high (this applies especially to *Cardium*). If we take it for granted that there is an effect of the substratum, this may make itself largely felt when the waddens are flooded twice every twenty-four hours owing to the tide, when considerable water masses, with the larvae found in them, come into close contact with the bottom. It may be imagined, therefore, that each time the waddens are flooded by a thin covering of water, they may actually draw larvae ready for settling out of the plankton.

3) Growth.—In most cases the brood exhibits a rapid growth in the course of the summer. In an annual species such as *Corophium volutator* the whole growth of course takes place within one season, and probably the growth of the small Polychaetes (*Pygospio* and *Polydora*) is likewise completed in the course of one season. Species which grow for more than one season in most cases exhibit a rapid growth during the summer half-year and a stagnation during the winter months. This is distinctly reflected in the growth diagrams for *Nereis diversicolor*, *Scoloplos armiger*, *Arenicola marina*, *Cardium edule*, *Hydrobia ulvae*, and *Littorina littorea*. *Hydrobia ulvae*, which may be regarded as a biological 1—1½ years' species, grows vigorously for two seasons. Two such important species as *Arenicola marina* and *Cardium edule*, which subsist for several years, grow most vigorously during their first two years, after which their growth is appreciably lower, and this probably applies to several perennials whose later growth it is impossible to find out. In *Cardium* the growth conditions are comparatively easy to ascertain, as the age-groups are distinguishable by distinct winter rings.

In the investigations of THAMDRUP (1935), and KREGER (1940), and in the present investigation it has been shown that *Cardium* grows the more rapidly the longer the submersion period lasts, and the same was shown by NEWCOMBE (1935) and WARREN (1936) for *Mytilus edulis*. THAMDRUP (l. c.), as an explanation of this growth in *Cardium*, states that it is a suspension feeder and accordingly depends on the submersion for its intake of food, and this explanation is further confirmed by the fact that *Mytilus*, too, is a suspension feeder.

4) Quantitative occurrence.—The large quantities of the youngest bottom stages occurring on the waddens in summer are of primary importance, as they constitute the main food of the young fish growing up in the Waddensea at this time of the year; however, the quantities of this brood vary from year to year. On the waddens the following species occur in abundance:

Nereis diversicolor as 0-group was found in a maximum number of 23,000 per m² (the wadden north of Fanø ¹⁸/₆ 1947).

Nephtys hombergi as 0-group was found in a maximum number of ca. 1000 per m² (on the wadden north of Fanø, ²²/₆ 1946).

Scoloplos armiger as 0-group was found in a maximum number of 29,400 per m² (on the wadden north of Fanø, ¹⁵/₄ 1948).

Pygospio elegans was not generally separated into juvenile and older individuals on sampling. On the wadden north of Fanø up to ca. 32,000 juvenile individuals per m² were found at a single station (²²/₆ 1946).

Polydora ligni (or *ciliata*?) was never secured in particularly large numbers (maximum 900 per m² on the wadden north of Fanø, ²²/₇ 1947), but no doubt it must be present in very large quantities in some localities, considering the abundance of pelagic larvae.

Heteromastus filiformis may occasionally occur in large numbers. The maximum number found was up to 2,200 per m² (the wadden north of Fanø, ¹⁰/₁₀ 1947).

Arenicola marina, which is of great economic importance, can never, owing to its size, be present in very large numbers. The greatest densities were observed by THAMDRUP (1935) on the wadden at Skallingen, viz. up to 70 juvenile and up to 35 older individuals per m².

Cardium edule, 0-group individuals often occur in numbers ranging between 20,000 and 30,000 per m², and as the maximum THAMDRUP (verbal information) in 1937 found nearly 100,000 per m² on Langli Sand.

Macoma baltica as 0-group was collected in numbers of up to 16,000 per m² (soft wadden at Nordby, ³⁰/₆ 1942).

Mya arenaria was found as 0-group in a maximum number of 43,000 per m² (the soft wadden at Nordby, ²²/₆ 1947).

Hydrobia ulvae may, as newly settled, occur in enormous numbers. The maximum number found was 663,000 per m² (the soft wadden at Nordby, ²³/₆ 1946). The maximum number of older individuals (mainly I-group) was 61,000 per m² (on the wadden north of Fanø, ²²/₆ 1946).

Corophium volutator was not sorted into juvenile and older individuals when counted. The maximum number in the Waddensea was 24,800 per m² (on the wadden off Hojer, August 1941).

In the channels it is chiefly *Crangon vulgaris* and *Mysis flexuosa* that are of importance as food, but it is impossible to give any figures for their quantitative occurrence. *Asteria rubens*, which has quite recently acquired economic importance, is present in enormous quantities in certain places, as shown by the fishery statistics (p. 90).

The young and the older individuals do not always have their maximum occurrence in the same places. As a rule this is due to the fact that the brood, where it is, at first, most numerous, is so greatly pursued by enemies that it is totally, or almost totally, exterminated. But in some cases migrations also take place. The best example of this is provided by *Arenicola marina*, whose youngest bottom stages are predominantly found on the inner zones of the waddens, while the older stages have their maximum farther out on the waddens. A migration in the opposite direction is found for *Hydrobia ulvae*, whose brood is numerous over the greater part of the waddens, while the older individuals are concentrated within the innermost zone of the waddens. It is true that the disappearance of the brood from the outer part of the waddens is principally due to the persecution by enemies, but it is also possible to demonstrate that an inward migration takes place. As to *Nereis diversicolor* something similar seems to be the case. It should also be noted that the broods of *Crangon vulgaris* and *Carcinus maenas* are of frequent occurrence on the waddens in summer and autumn, when they are probably less exposed to the persecution by enemies than in the channels.

5) Mortality.—During the development from the egg to the adult bottom animal a high degree of mortality will naturally be found among the immense quantities of brood produced. For the species which have a long pelagic development a very heavy reduction takes place at this stage as compared with other species which have a much shortened pelagic or a non-pelagic development (see under 1, comparison between Lamellibranchs and *Hydrobia ulvae*). The heavy mortality of the Lamellibranchs from egg to bottom stage is due to the cir-

cumstance that both eggs and larvae are pelagic, and the fact that *Pygospio* and *Polydora*, which produce few eggs compared with the Lamellibranchs, are capable of sending out so many larvae into the plankton, can be explained by the fact that during the whole embryonic development the eggs are well protected in the tubes of the mother animals.

The high mortality among the youngest bottom stages as a result of the persecution by enemies, is distinctly revealed by the quantitative investigations.

In addition to this normal mortality, such catastrophes as severe winters may have a very destructive effect. A typical example of this was the total extermination of the population of *Cardium edule* on the waddens in the winter of 1946—47. But other species, also, may suffer in severe winters (cf. SMIDT 1944 B).

VIII. Composition and Variation of the Zooplankton, with special reference to the pelagic bottom animal larvae.

In the years 1942, 1943, 1944, 1946, and 1947 plankton samples were collected for the purpose of acquiring knowledge of the quantitative occurrence of the bottom animal larvae which are produced in the Waddensea proper and those which are carried in from the sea outside and do not occur in the area as adults¹). At the same time the occurrence of other planktonic organisms was noted down also.

A. Zooplanktonic organisms with the exception of the bottom animal larvae.

Noctiluca miliaris SURIR.

Noctiluca was found in the period May—January, but not in February, March, and April. It was most numerous and most frequent in the high-water samples.

Hydromedusae.

Various species were found in the period March—December, but they were only frequent in the period April—August (September). They occurred most frequently in the high-water samples.

Scyphomedusae.

The following species, which were not taken with the plankton bag, were occasionally observed swimming in the water: *Cyanea capillata* (L.) and *Aurelia aurita* (L.) are of common occurrence in the summer months. *Rhizostoma pulmo* (L.) is frequent in the autumn, and *Chrysaora hysoscella* (L.) was observed on one occasion only (7/11 1945).

Pleurobrachia pileus (O. F. MÜLLER).

The species was met with at all seasons of the year, but it was most numerous in the summer months. It was chiefly found in the high-water samples, having only on rare occasions been observed in low-water samples.

¹ Tables showing the numbers of bottom-animal larvae found in the plankton-samples are kept at the Marine Biological Laboratory.

Rotatoria.

Found in the period March—November, but were most numerous in the months May—October. They were abundant in both high-water and low-water samples.

Turbellaria.

A few individuals were observed swimming in high-water samples taken in May, August, and October.

Autolytus.

A few individuals were occasionally observed in both high-water and low-water samples in the period April—November. The following two species were determined by E. WESENBERG-LUND: *Autolytus (Polybostrichus)* and *Sacconereis* *prolifer* (O. F. MÜLLER) and *Autolytus (Polybostrichus)* *prismaticus* (O. FABRICIUS).

***Podon* sp.**

Observed in the months April—August and once in January. It chiefly occurs in the high-water plankton. In most samples it was sparsely present, but a single sample contained 126 per m³ of water (high-water sample, ⁶/₆ 1942).

***Evadne* sp.**

Small numbers collected in the period April—October, chiefly found in high-water samples.

Copepoda.

Copepoda occur at all seasons of the year, but are most numerous in summer and autumn and have their minimum in January—February—March. In addition to the actual pelagic Copepods, many *Harpacticoidea* occur, which have been whirled up from the bottom with bottom material. In 1942 the *Harpacticoidea* constituted ca. 24 per cent. of the Copepods counted in the high-water samples and 46 per cent. in the low-water samples. Generally the Copepods were more numerous in the high-water than in the low-water samples, thus, in 1942 ca. 84 per cent. of the pelagic Copepods were found in the high-water samples, and in 1943 63 per cent. As regards the *Harpacticoidea*, in 1942 ca. 66 per cent. of the individuals counted were found in high-water samples (possibly some have been overlooked in the low-water samples as these contained much detritus). Copepod larvae occur in varying quantities at all seasons of the year, but they are most numerous in the summer half-year.

As the Copepods constitute a group which is very abundantly represented in the plankton, and as they are of importance as food for the herring fry which frequents the Waddensea in the summer, their numbers per m³ of water in sample material from 1942 and 1943 will be given in table 6.

***Sagitta* sp.**

Taken in the period May—January with a maximum in September. In most samples only a few individuals were present; the maximum number was 51 per m³ of water (high-water sample, ²⁷/₉ 1943). The majority (ca. 87 per cent.) occurred in the high-water samples.

Table 6. *Copepoda* (number of individuals per m³ of water) in the plankton off Esbjerg at high and low tides (H and L) in 1942 and 1943.

1942												
Month.....	Apr.		May		June		July		Aug.		Aug.	
Date.....	3	3	15	16	6	6	2	2	1	1	19	19
Water level.....	H	L	H	L	H	L	H	L	H	L	H	L
Pelagic Copepoda.....	110	80	136	63	3400	92	157	173	970	96	244	295
Harpacticoidea.....				+	41	15	46	53	50	84	240	202
Nauplia.....	78	28	83	72	938	38	695	20	56	620	100	270
1942												
Month.....	Aug.		Sep.		Oct.		Nov.		Nov.		Dec.	
Date.....	29	29	17	16	7	7	2	1	24	24	21	22
Water level.....	H	L	H	L	H	L	H	L	H	L	H	L
Pelagic Copepoda.....	487	86	720	344	225	62	223	50	122	52	15	10
Harpacticoidea.....	187	97	146	395	420	194	100	10	20	26	18	10
Nauplia.....	400	147	472	52	238	379	250	63	+	+	16	+
1943												
Month.....	Jan.		Feb.		Mar.		Apr.		May		June	
Date.....	7	8	23	23	21	21	20	20	20	20	20	21
Water level.....	H	L	H	L	H	L	H	L	H	L	H	L
Pelagic Copepoda.....	21	11	48	50	73	44	144	85	457	155	106	37
Nauplia.....	10	+	30	66	50	14	540	85	+	—	50	59
1943												
Month.....	July		Aug.		Aug.		Sep.		Oct.		Dec.	
Date.....	19	19	3	3	29	30	27	27	31	31	6	5
Water level.....	H	L	H	L	H	L	H	L	H	L	H	L
Pelagic Copepoda.....	127	66	142	124	980	825	515	253	200	70	77	17
Nauplia.....	33	22	91	124	125	473	211	110	447	22	125	11

Copelata.

Found in the period May—November, most frequently in August—October. The majority (ca. 88 per cent.) were taken in high-water samples, and the maximum number was 242 per m³ of water (high-water sample, 7/10 1942).

Whirled-up bottom animals.

A number of small bottom animals which had been whirled up in the water with bottom material, were observed. Newly settled *Ophiura* were observed in the summer of 1942 (high-water samples, 21, 7 and 1/8). Of newly settled Lamellibranchs the following species were observed: *Cardium edule*, *Macoma baltica*, *Mya arenaria*, *Mytilus edulis*, and *Montacuta bidentata*. Further, on a few occasions in summer and autumn some *Cumaceae* and *Acarinae* were found.

B. Bottom animal larvae.**ANNELIDA.**

The following species have already been treated in the preceding chapter: *Eteone longa*, *Phyllodoce maculata*, *Nereis diversicolor*, *Nephtys hombergi*, *Pygospio elegans*, *Polydora ligni* (= *ciliata*?), *Arenicola marina*, *Capitella capitata*, *Heteromastus filiformis*?, and *Pectinaria koreni*.

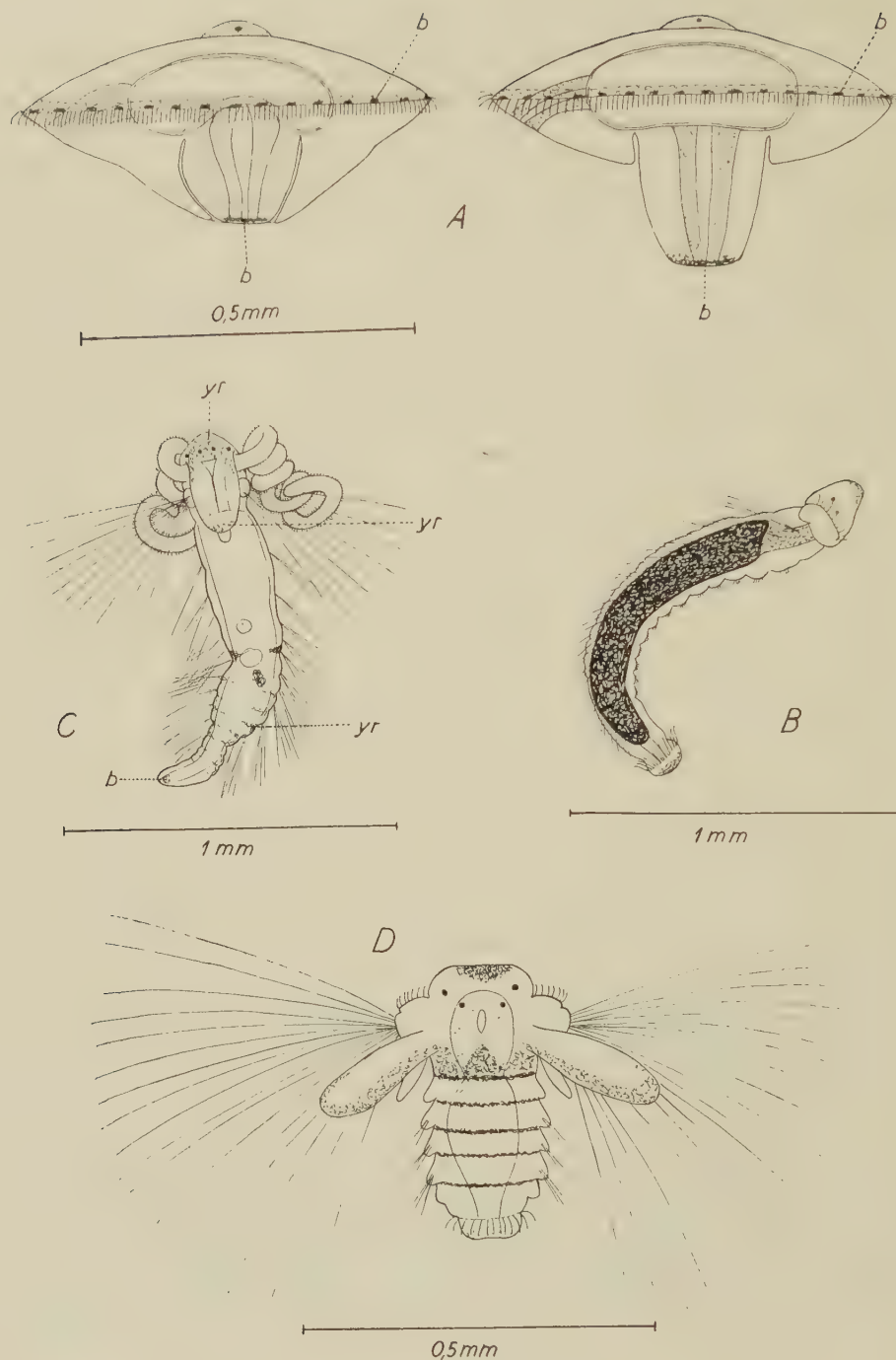


Fig. 36. A: *Polygordius* sp.: *Trochophora* from high-water plankton taken off Esbjerg on $20/6$ 1943 (drawn from life; to the left with withdrawn, to the right with projecting hind part). — B: *Spionid* sp. larva, type X from high-water plankton taken at the pier at Esbjerg on $18/6$ 1943 (drawn from life). — C: *Magelona papillicornis*: larva from Graadyb, $2/7$ 1943 (drawn from life; *Mytilus* larvae are seen in the intestine). — D: *Sabellaria spinulosa*: larva from high-water plankton taken at the pier at Esbjerg on $17/6$ 1943 (drawn from life; long bristles on the anterior segment finely serrated, pigmentation black). — Pigmentation: b = black, yr = yellowish-red.

***Polygordius* sp.**

On some occasions a few *Trochophora* were taken in high-water samples (1943: $^{29}/_8$, 1946: $^{8'}/_9$ and $^{12}/_{10}$). They must be assumed to have been carried into the Waddensea with the flood-tide. In fig. 36A a specimen is shown which was kept in the laboratory for a couple of days. The larva was at first lens-shaped, but after a few hours the withdrawn posterior end was ejected. Along the prototroch a stripe of yellow pigment was seen, and inside this a row of black pigment spots. A little black pigment was seen around the anus. Two eye spots were visible on the apical plate.

***Polynoid* sp.**

A few larvae (possibly *Harmothoe*) were observed in the plankton at different times of the year: 1943: $^{31}/_{10}$ (high-water); 1946 $^{8}/_8$ (high-water and low-water), $^{12}/_{10}$ (high-water); 1947: $^{31}/_3$ (high-water), $^{22}/_3$ (high- and low-water). Probably some of them had been produced in the Waddensea.

Unknown *Spionid* larvae.

Type B, which is identical with the "spionid-larva B" described and figured by THORSON (1946) was taken occasionally in a few specimens both in low-water and high-water samples: 1942: $^{6}/_6$ (high-water), $^{19}/_8$ (high-water); 1943: $^{20}/_5$ (high- and low-water), $^{19}/_7$ (high-water), $^{30}/_8$ (low-water).—Type X (fig. 36B) was collected once in high-water plankton $^{18}/_6$ (1943). The larva had a black intestine and a verdigris-coloured oesophagus; some verdigris-coloured pigment was likewise found posteriorly.

***Scolecoplepis squamata* (ABILDG.), Syn.: *Nerine cirratulus* (AUD. & EDW.).**

Some *Trochophora* surrounded by a reticulate egg membrane, corresponding to those described and figured by CUNNINGHAM & RAMAGE (1888) and CLAPAREDE & METSCHNIKOFF (1869), were observed on several occasions in April—May and once in July. The maximum number present was 40 per m³ of water ($^{20}/_4$ 1943, high-tide). As a rule the larvae were most numerous in the high-water samples. There is every reason to assume that they were produced immediately outside the Waddensea or in the outer part of this sea, for the adults are most numerous along the west coast of Fano (and probably along the west coasts of the other islands and Skallingen, also), while in the Waddensea they were only observed in the outer portion (the sand wadden east of Skallingen) and in small numbers only.

***Magelona papillicornis* (O. F. MÜLLER).**

Pelagic larvae (fig. 36 C) which agree entirely with those previously described and figured (cf. THORSON 1946), were fairly frequently met with in plankton samples taken in the period May to the beginning of November. The great majority were found in high-water samples, only twice some few individuals were present in the low-water samples. The maximum number was 177 per m³ of water (high-water sample, $^{20}/_6$ 1943). It may be taken for granted that the larvae are chiefly produced outside the Waddensea (adult individuals were only observed once and in a very small number in the Waddensea). Like previous authors (LEBOUR 1922, THORSON 1946), the present author, also, found Lamellibranch larvae in the stomachs of *Magelona* larvae.

***Owenia fusiformis* DELLE CHIAJE.**

A few "*Mitraria*", probably belonging to this species, were found in plankton samples $^{15}/_5$ – $^{16}/_5$ 1942 (both at high and at low tide). The larvae are probably produced outside the

Waddensea, for adults have not been taken within the area, but occur outside, in the North Sea (unpublished material at the Danish Biological Station).

***Lanice conchilega* (PALLAS).**

The larvae (fig. 37), which are surrounded by thick gelatinous tubes, agree closely with the descriptions and figures published by previous authors (cf. THORSON 1946). Characteristic of the larval tubes is a distinct structure of obliquely placed layers. The larvae occurred mainly in the high-water samples, but were also represented in the low-water samples. The

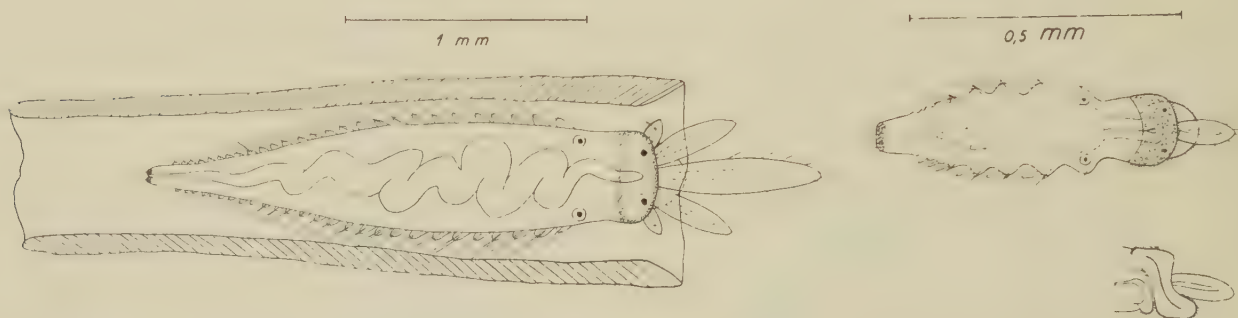


Fig. 37. *Lanice conchilega*: Right: young larva removed from its slime tube. Plankton sample taken off Esbjerg on $^{10}/_7$ 1942. — Left: older larva in its slime tube. Plankton sample taken near Esbjerg on $^{21}/_7$ 1942. Both drawn from life. Pigmentation on head and posterior end dark brown.

maximum number found was 106 per m^3 of water (high-water sample, $^{20}/_6$ 1943). Their occurrence would seem to suggest that the main production takes place outside the Waddensea or in its outer part, but since the adults, besides occurring outside the Waddensea, are present within the area, no small larval production undoubtedly takes place in the Waddensea.

***Sabellaria spinulosa* LEUCK.**

The larvae (fig. 36 D), which have been described by WILSON (1929), occurred in the plankton samples in the period April—December, but they are abundant in the summer and autumn, only. Their maximum number was 67 per m^3 of water (high-water sample, $^{12}/_{10}$ 1946). They occurred most frequently and most abundantly in the high-water samples, which agrees with the assumption that the main production takes place in the deeps leading to the Waddensea, for according to the reports of fishermen, large quantities of “sand corals” (blocks of sand tubes cemented together) are present in these deeps.

Undetermined *Trochophora*.

Various unidentifiable *Trochophora* occur in varying quantities at different times of the year, sometimes in very large numbers.

2) NEMERTINI.

A few undetermined “*Pilidium*” were observed on rare occasions in high-water samples (1942: $^6/_6$ and $^{24}/_{11}$; 1943: $^{27}/_9$; 1944: $^{19}/_3$).

3) TENTACULATA.

Phoronis sp.

"*Actinotrocha*" were found on a few occasions in plankton samples in September, October, and December. They were taken three times in high-water samples and once (a single individual) in a low-water sample. Probably the larvae had been carried in from the outside by the current.

Membranipora.

A small grey "*Cyphonautes*" with a granulated structure (fig. 38 A), entirely resembling "*Cyphonautes barroisi*" LOHM. (cf. MARCUS 1940), was observed in all the months of the year, but most numerous in summer and autumn. The maximum number found was 233 per m³ of water (²⁷/₉ 1943, high-water sample). It was of frequent occurrence in high-water as well as in low-water samples, and it must be assumed to be largely produced in the Waddensea. In the samples counted it proved to be a little more numerous in the high-water samples (⁵⁹/₀) than in the low-water samples, but owing to its small size and inconspicuous appearance there is a great probability that a number of them have been overlooked in the low-water samples,

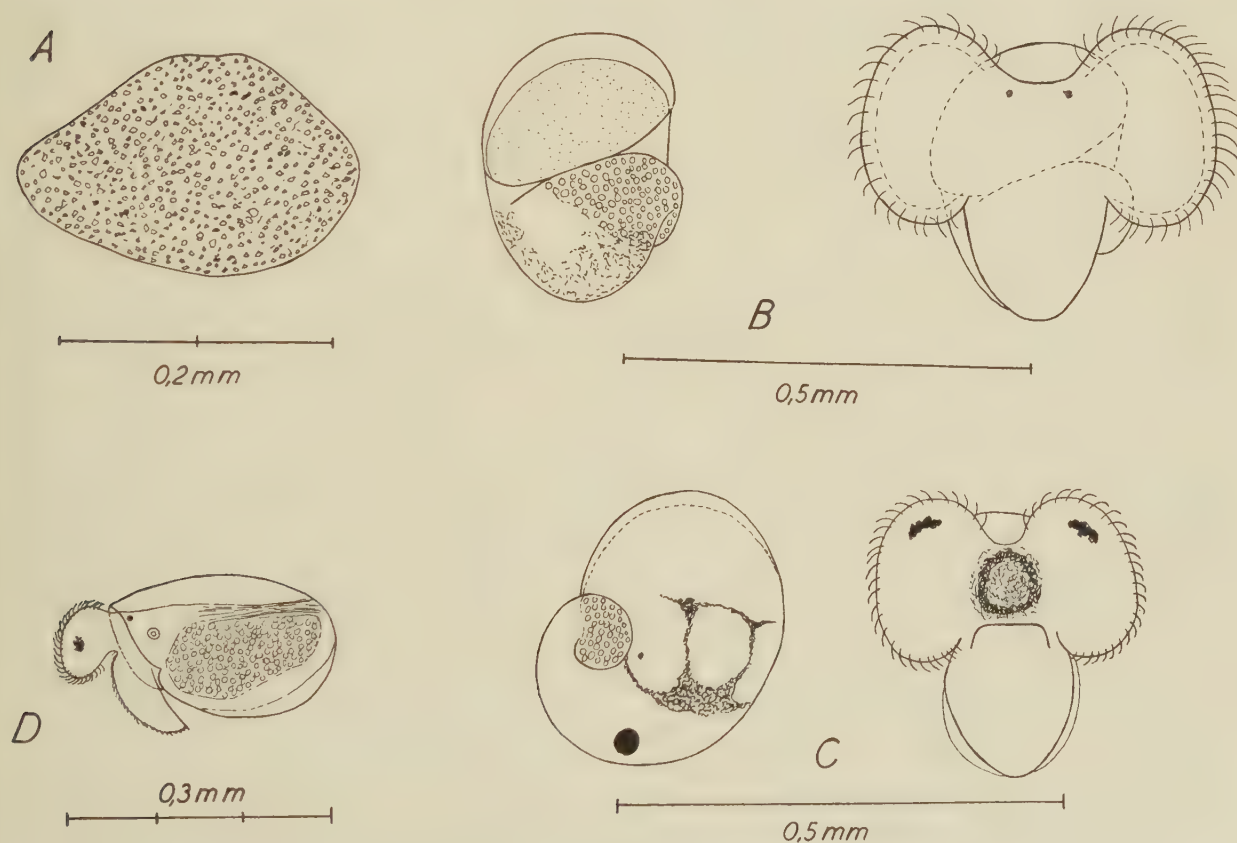


Fig. 38. A: *Cyphonautes barroisi* from plankton taken off Esbjerg on ²⁷/₅ 1944 (drawn from preserved specimen). — B: *Retusa truncatula*: larva taken in plankton off Esbjerg on ²⁹/₈ 1943 (drawn from life). — C: *Limapontia capitata*: Larva taken in plankton over the wadden north of Fanø on ²¹/₁₀ 1946 (drawn from life; excretion organ and pigmentation on velum and around the mouth black). — D: *Nudibranch* sp.: Larva from high-water plankton taken off Esbjerg on ²⁹/₈ 1943 (drawn from life; on the velum a faint dark pigmentation).

these samples containing much detritus. MARCUS (1940) is of the opinion that the larva is referable to *Membranipora crustulenta*, which was also found in the Waddensea. But since by far the commonest species within the area is *M. reticulum*, the possibility should be kept in view that the larva figured here may belong to that species. It is also possible that the larvae of the two species bear such a close resemblance to each other that they are difficult to distinguish from one another.

In addition to the above-mentioned larvae, a few larger "*Cyphonautes*" were occasionally observed in the period March—January, chiefly in the high-water samples.

4) GASTROPODA.

Littorina littorea and *Hydrobia ulvae* were mentioned in the preceding chapter.

Onoba vitrea MONTAGU.

A single larva corresponding to that described and figured by THORSON (1946) was found in a low-water sample on $^{24}/_{11}$ 1942.

Coecum glabrum (MONTAGU).

A few *Coecum* larvae were observed in high-water samples on $^{8}/_{8}$ 1946 and $^{12}/_{10}$ 1947. As *C. glabrum* is the commonest species in the North Sea (i. a. it is numerous in the deep channel at Heligoland (ANKEL 1936)), it is probable that the larva belongs to this species.

Pyramidellid sp.

A single sinistrorse larva of the *Pyramidellid* type, possibly *Odostomia* sp., was found in a high-water sample on $^{17}/_{9}$ 1942.

Nassa reticulata LINNÉ.

A single larva was taken in a low-water sample on $^{8}/_{8}$ 1946. Possibly it had been produced within the area, for adult specimens have been taken in the German Waddensea near Sylt (HAGMEIER & KÄNDLER 1927, WOHLLENBERG 1937), and probably it may be met with in the Danish Waddensea also.

Bela turricola (MONTAGU).

VESTERGAARD (1935) describes the egg capsule and the youngest larval stage of this species. The larvae had a smooth transparent shell, and were characteristic by having a bi-lobed velum with big lemon-coloured spots along the margin. On the sides of the elongate foot there was a reddish pigment, which in the course of a few days turned darker. The oral orifice, statocysts, eyes, and right tentacle were distinctly seen. The larvae from the Waddensea shown in fig. 39 so closely resemble that described above that they may be regarded as older larval stages of *Bela turricola*, which as adult is very common in the North Sea outside the Waddensea (BLEGVAD 1922, HAGMEIER 1925, unpublished data supplied by the Danish Biological Station). The larvae have a big, flat-spined, smooth, and transparent shell. Along the margin of the two-lobed velum a stripe of dark purple pigment is seen, and inside this there is, in the younger stage, a row of big yellow pigment spots, which in the older stage have united so as to form a broad yellow band; at the same time several yellow spots have appeared on the inner part of the velum. The broad stout foot exhibits some dark purple pigment on the sides and in a stripe on the middle, and in between these, on either side, a series of yellow pigment spots. The tentacles, eyes, and statocysts are distinctly visible, and the oral orifice markedly dark-pigmented.

This larva was observed in small numbers on a few occasions in high-water samples from the months June–September (in samples taken off the harbour of Esbjerg on $\frac{3}{8}$ and $\frac{29}{8}$ 1942, $\frac{8}{9}$ 1946, and $\frac{23}{7}$ 1947, further, in plankton samples collected over the wadden

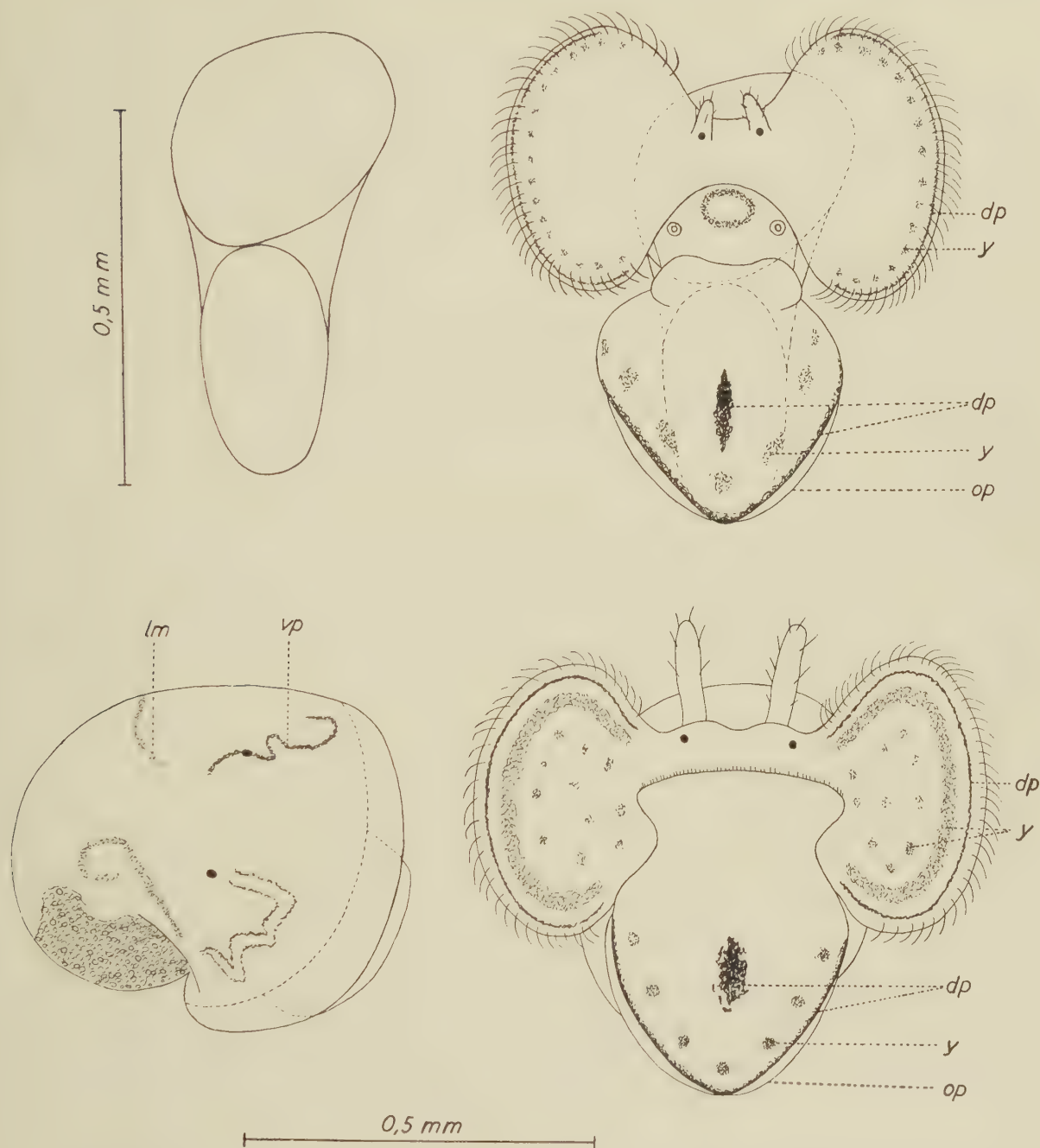


Fig. 39. *Bela turricola* ?. Late larval stages. Above: younger stage from plankton taken over the wadden northeast of Fanø on $\frac{9}{8}$ 1946. — Below: older stage from high-water plankton taken off Esbjerg on $\frac{20}{8}$ 1943. — (Both drawn from life; dp = dark purple and y = yellow pigmentation; vp = velar pigment, lm = mantle limit, op = operculum).

northeast of Fano on $9/8$ 1946 and $18/6$ and $29/8$ 1947). The occurrence of the larvae in only high-water samples and their large size as well as the absence of the adults from the Waddensea support the assumption that they had been carried in with the current from the sea outside.

***Retusa truncatula* (BRUGUIRE).**

The larva represented in fig. 38 B agrees closely with the larva of *R. truncatula* described and figured by THORSON (1946). The shell is transparent and sinistrally twisted and with a wide mouth. The velum is two-lobed and without pigment. The liver is yellowish-brown, and on the mantle there is a scattered dark violet pigmentation. Small numbers of the larva were collected on a few occasions in high-water samples in July, August, and September. The adults possibly occur in the Danish Waddensea, but were not observed. The *R. obtusa* occurring on the waddens has a non-pelagic development (cf. THORSON l. c.).

***Philina aperta* (LINNÉ).**

Larvae which agree closely with that described and figured by THORSON (1946) were observed on a few occasions in the period June—October, and a single doubtful specimen was found in April 1944. They were most frequent and most numerous in the high-water samples (maximum number found 28 per m^3 of water in a high-water sample on $17/9$ 1942), and as adult individuals are not known from the Waddensea, the larvae must be assumed to have been transported in with the current from the sea outside.

***Limapontia capitata* (MÜLLER).**

Pelagic larva (fig. 38 C) (described and figured by THORSON (1946)) were observed singly or in small numbers at almost all times of the year in high-water as well as in low-water samples. The adults were not observed in the Danish Waddensea, but probably they were overlooked, for they have been observed in the German Waddensea in the *Salicornia-Zostera* zone at Sylt (WOHLENBERG 1937). Probably some of the larvae had been produced in the Waddensea.

Other *Ascoglossa* sp.

Larvae with sinistral shells closely resembling the larval shells of *Limapontia* were observed singly in high-water samples on $27/9$ 1943 and $19/8$ 1944.

***Nudibranch* sp.**

Nudibranch larvae (fig. 38 D) in small numbers were observed on several occasions in the period June—January, most frequently in high-water samples. The maximum number was 13 per m^3 of water (high-water sample, $8/8$ 1946).

5) LAMELLIBRANCHIA.

In the determination of the larvae I have been assisted by C. BARKER JØRGENSEN. The species *Mytilus edulis*, *Cardium edule*, *Macoma baltica*, and *Mya arenaria* have already been treated in the preceding chapter. In addition to the literature quoted below, a paper on Lamellibranch larvae has recently been published by REES (1950).

***Venus gallina* L.**

The larva, which is described and figured by BARKER JØRGENSEN (1946), was taken in a high-water sample on $23/7$ 1947 (determination not quite certain). As adult individuals

were not found in the Waddensea, but are of very common occurrence in the North Sea outside, where they form communities (BLEGVAD 1922, HAGMEIER 1925, unpublished data recorded at the Danish Biological Station), it is highly probable that the larvae have been carried in with the current from the sea outside.

***Montacuta bidentata* MONTAGU.**

The determination was made after BARKER JØRGENSEN (1946). Some larvae were taken in high-water samples on $17/9$ 1942 (one) and $27/9$ 1943 (22 per m^3 of water). In addition to the pelagic larvae, some newly settled ones, whirled up in high-water plankton, were found on $29/8$ 1943. The occurrence of adults in the Waddensea was not ascertained, but they may have been overlooked owing to their diminutive size.

***Tellinidae* and *Semelidae*.**

Some oval larvae, considered by BARKER JØRGENSEN to belong to *Tellina* or *Syndosmya*, were found in a high-water sample on $6/12$ 1943 in a number of 25 per m^3 of water. Species of the genera *Syndosmya* and *Tellina* are very common outside the Waddensea; further, *Tellina tenuis* occurs in small numbers in the Waddensea proper, and *Syndosmya alba* was taken by HAGMEIER and KÄNDLER (1927) on the *Ostrea* banks in the German Waddensea.

***Spisula subtruncata* (DA COSTA).**

The larvae, determined after BARKER JØRGENSEN (1946), were occasionally observed in high-water samples in the period July—October. The maximum number found was 97 per m^3 of water (high-water sample $19/7$ 1943). The larvae had probably been produced outside the Waddensea, where the adults are of common occurrence (BLEGVAD 1922, HAGMEIER 1925, unpublished material at the Danish Biological Station); however, adults have also been taken in small numbers on oyster banks in the German Waddensea near Sylt (HAGMEIER & KÄNDLER 1927).

***Mya truncata* (L.)**

The larvae are described and figured by BARKER JØRGENSEN (1946). In a high-water sample taken on $17/9$ 1942 several larvae were found (22 per m^3 of water) which were apparently referable to this species. According to WOHLBERG (1937) the adults occur in the German Waddensea below the low-water mark.

***Zirphaea crispata* L.**

The larvae have been described and figured by WERNER (1939) and BARKER JØRGENSEN (1946). They were found in small numbers in eleven high-water samples in the period April—December. The maximum number was 15 per m^3 of water ($20/4$ 1943). According to HAGMEIER & KÄNDLER (1927) adults occur now and then in submarine peat in the Waddensea, but the majority of larvae may have been carried in with the current from the North Sea, where adults are common in moor logs.

***Teredo* sp.**

A single larva from a high-water sample taken on $8/9$ 1946 was referred with doubt by BARKER JØRGENSEN to the genus *Teredo*.

Big unknown larvae.

A number of fairly big larvae in the samples could not be determined, either because they were not identified, or because they were in a poor state of preservation.

Small indeterminable larvae.

These larvae, which were at times very numerous in both high-water and low-water samples, varied greatly in number in the course of the year (cf. also the preceding chapter p. 91).

6) CRUSTACEA.

This group has been treated in the preceding chapter (p. 87—89).

7) ECHINODERMA.

All the larvae were determined after MORTENSEN (1924). *Asterias rubens* has been treated in the preceding chapter (pp. 89—90).

Ophiotrix fragilis ABILDG.

A single larva was taken in a high-water sample on ¹⁹/₇ 1943. Adults were not taken in the Waddensea, but occur in the North Sea (MORTENSEN 1924).

Ophiura texturata LAMARCK.

In the period May—August larvae occurred rather frequently in the high-water samples, but were only once taken in a low-water sample. The maximum number found was 160 per m³ of water (high-water sample ¹⁴/₇ 1942). Adults are of common occurrence in the North Sea (HAGMEIER 1925; unpublished material at the Danish Biological Station), but have only been observed in small numbers in the German Waddensea (LINKE 1939). Hence it must be taken for granted that the larvae are mainly produced outside the Waddensea. Some newly settled specimens were found off the harbour of Esbjerg, whirled up into high-water plankton, on ²¹/₇ and ¹/₈ 1942.

Ophiura albida FORBES.

Larvae in small numbers were occasionally observed in high-water samples in May and September. Adults are common in the North Sea (HAGMEIER 1925; unpublished material at the Danish Biological Station), while only a few were observed in the Waddensea (HAGMEIER & KÄNDLER 1927). Accordingly the larvae must be regarded as produced in the North Sea.

Echinus esculentus (LINNÉ).

On rare occasions a few larvae were found in high-water samples in the period May—August. A few adult individuals have been taken on an oyster bank in the German Waddensea (HAGMEIER & KÄNDLER 1927).

Psammechinus miliaris (GMELIN).

Some few larvae were occasionally found in high-water samples in the period June—September. The maximum number registered was 13 per m³ of water (¹²/₇ 1944). As adults are common in the channels in the Waddensea, a certain production probably takes place within the area.

***Echinocardium cordatum* (PENNANT).**

Larvae were occasionally found in high-water samples in the period May—July. The maximum number found was 53 per m³ of water (¹⁵/₅ 1946). Adults have not been found in the Waddensea, but outside it, in the North Sea, they are very common (HAGMEIER 1925; unpublished material at the Danish Biological Station). The larvae must be assumed to have been carried in from the sea outside with the current.

Summary and discussion.

1) General characterisation of the zooplankton. The zooplankton of the Waddensea is poor in species. Thus hardly sixty species of bottom animal larvae were found, while in the Sound, according to THORSON (1946), about 160 species have been observed.

It is characteristic of the plankton of the Waddensea that it varies with the tidal currents. In chapter III it was mentioned that owing to the tide there is a lively exchange of water between the Waddensea and the North Sea, and as a result of this many organisms produced in the Waddensea are carried out into the North Sea, while at the same time many are transported into the Waddensea from the outside. To give an idea of the distance a water mass may travel during one tidal period, it was mentioned that a water mass which at high tide is found off the harbour of Esbjerg, at the succeeding low tide may be found right outside Graadyb, that is, in the North Sea. And, as a matter of fact, a number of planktonic organisms were far more frequent and more numerous in the high-water samples than in the low-water samples, viz. *Noctiluca*, *Pleurobrachia*, *Podon*, *Evadne*, *Sagitta*, *Copelata*, and several bottom animal larvae (see below).

It is further characteristic of the plankton of the Waddensea that owing to the strong tidal current a large quantity of bottom material is whirled up in the water, and together with it a number of bottom organisms which set their stamp on the plankton samples. Thus several *Harpacticoidea* were present in the samples, but other small bottom animals, i. a. a good deal of newly settled bottom animal brood, are met with in the plankton.

The largest quantities of suspended bottom material were found in low-water samples, probably because it had been washed out from the waddens by the ebb-tide, and this suspended material may, no doubt, be of a certain significance for the results of the investigations, the chance of overlooking small organisms being considerably greater in low-water plankton than in high-water plankton. As mentioned in the preceding chapter, the fact should also be taken into consideration that many small plankton organisms, notably Lamellibranch larvae, are eaten by the many Spionid larvae that occur in the low-water plankton.

2) Exchange of bottom animal larvae between the Waddensea and the North Sea.—Between the *Macoma baltica* community of the Waddensea and the communities in the North Sea outside an exchange of pelagic larvae takes place. The communities of the Waddensea continue in a narrow zone outside the islands, but beyond these, in deeper water, there is a zone with a *Syndosmya* community, which in the Heligoland Bay has a wider distribution. Outside this, an extensive *Venus* community occurs. (Information about these communities was obtained from BLEGVAD 1922, HAGMEIER 1925, and unpublished material at the Danish Biological Station).

A considerable number of the larvae which are produced in the Waddensea and are carried with the ebb-tide into the North Sea, will there, when the water of the Waddensea is

mixed with that of the North Sea, be lost to the Waddensea, but a great part may be carried in again with the flood-tide. The following larvae are mainly or largely produced in the Waddensea: *Annelida*: *Eteone longa*, *Phyllodoce maculata*, *Nereis diversicolor*, *Nephtys hombergi*, *Pygospio elegans*, *Polydora (ligni?)*, *Arenicola marina*, *Capitella capitata*, *Heteromastus filiformis?*, *Pectinaria koreni*; *Tentaculata*: "*Cyphonautes barroisi*"; *Gastropoda*: *Littorina littorea*, *Hydrobia ulvae*; *Lamellibranchia*: *Mytilus edulis*, *Cardium edule*, *Macoma baltica*, *Mya arenaria*;—*Crustacea*: *Balanus* sp. sp., *Crangon vulgaris*, *Carcinus maenas*, *Mysis flexuosa*;—*Echinoderma*: *Asterias rubens*, *Psammechinus miliaris*.

To the larvae which are produced outside the Waddensea or in its outer parts (i. a. the deeps between the islands) the following must be referred: *Annelida*: *Polygordius* sp., *Scolecoplepis squamata*, *Magelona papillicornis*, *Owenia fusiformis*, *Lanice conchilega*, *Sabellaria spinulosa*;—*Tentaculata*: *Phoronis* sp.;—*Gastropoda*: *Coecum glabrum*, *Bela turricola*, *Philine aperta*;—*Lamellibranchia*: *Venus gallina*, *Tellinidae* sp., *Spisula subtruncata*, *Zirphaea crispata*;—*Echinoderma*: *Ophiothrix fragilis*, *Ophiura texturata* and *albida*, *Echinus esculentus*, *Echinocardium cordatum*.

3) Occurrence of the larvae in the course of the year.—On counting the plankton samples it turned out that a minimum of larvae occurred in January–February, while in the following months the number of species as well as the number of individuals increased. In all the years during which my studies were carried on, larvae of the following species began to appear even before May 1st: *Phyllodoce maculata*, *Pygospio elegans*, *Heteromastus filiformis?*, *Balanus* sp. sp., and in addition a number of small indeterminable Lamellibranch larvae. Further, in most of the years larvae (or eggs) of the following species were observed before May 1st: *Polydora (ligni?)*, *Scolecoplepis squamata*, *Littorina littorea* (eggs or larvae), and *Asterias rubens*. Finally, it should be mentioned in this connection that *Scoloplos armiger*, which has a non-pelagic development, spawns in March–April, and that the egg-capsules of *Hydrobia ulvae*, larvae of which were not observed, are present in large numbers in April. All these species, with the exception of *Asterias rubens*, have their main occurrence in the tidal area, i. e. on the waddens, where the rise of the temperature in spring soon exerts its influence (it was mentioned in chapter III that by the middle of April a temperature of ca. 20° C. was registered in a thin water-covering over the wadden, while the surface water at Esbjerg at the same time had a temperature of only 9.6° C.). During the following months the numbers of both species and individuals of pelagic larvae increase, but decrease again in the autumn. It is noteworthy that *Arenicola marina*, which is a typical inhabitant of the waddens, spawns in the autumn, but, being deeply buried in the bottom, it hardly feels the heating of the wadden surface in spring.

4) Settling of larvae in the Waddensea.—In the preceding chapter mention is made of the immense quantities of brood that may settle on the waddens, and the importance that must be ascribed to the effect of the substratum on the settling of the larvae. But besides this enormous settling of the Waddensea's own stock of larvae, a certain settling of larvae coming from the outside may take place; however, these latter must for the most part be regarded as doomed to death. An example of this was observed in the summer of 1942, when after an abundant occurrence in the plankton of *Ophiura texturata* larvae, a great many newly settled *Ophiura* were found whirled up in the water off the harbour of Esbjerg. As no adult *Ophiura* were observed in any of the samples taken with the bottom sampler or dredge in this water, it can be taken for granted that the young bottom stages soon perish.

5) Consumption of plankton animals.—In the preceding chapter the mortality among planktonic bottom animal larvae owing to persecution by enemies was discussed under B 1) and 2). Considering the plankton as a whole, the many small herrings (*Clupea harengus*, and possibly *C. sprattus* also) which occur in the Waddensea in summer, must be regarded as large-scale consumers. Thus fifteen small herrings between 4 and 5 cm long and caught on ³/₉ 1945 all had their stomachs filled with pelagic Copepods (on an average 40—50 Copepods per stomach). Besides the Copepods, it must be assumed that a quantity of *Balanus* larvae and other larger bottom animal larvae abounding within the area are consumed in quantity by these young herrings.

IX. Food of the Animal Fauna of the Bottom.

Reproduction, one of the two fundamental aspects of production, having been treated in the two preceding chapters, the other aspect, that of food, will be briefly dealt with below on the basis of the available literature, the author having made no studies within this field.

A. Types of feeders.

A good description of the feeding types is given by THAMDRUP (1935), and on the basis of this the subjoined survey was prepared. THAMDRUP distinguishes, after HUNT (1925), between suspension feeders and deposit feeders. According to REMANE (1933), the suspension feeders may be subdivided into “Strudler”, “Filtrierer”, and “Sedimentierer” (not represented in the Waddensea). The deposit feeders may be subdivided into “Taster” and bottom feeders. These types may be designated collectively as particle feeders, and in addition carnivores and omnivores occur.

Particle feeders	{	suspension feeders	{ “Strudler” (REMANE)
			{ “Filtrierer” (REMANE)
	{	deposit feeders	{ “Taster” (REMANE)
			{ bottom feeders

Preyers and omnivores.

The most important species from the point of view of production and consumption can—mainly according to THAMDRUP (l. c.), BLEGVAD (1914), and LINKE (1939)—be referred to one or several of these groups.

Polychaeta.—*Nereis diversicolor* may most precisely be characterised as omnivorous, as it feeds on bottom material, diatoms, plant fragments, smaller animals, and carcasses (BLEGVAD l. c.). *Nephtys hombergi*, according to BLEGVAD (l. c.), is carnivorous. *Scoloplos armiger*, *Heteromastus filiformis*, and *Arenicola marina* are indiscriminate bottom feeders, and *Pygospio elegans* is referred to the “Taster” (THAMDRUP l. c.). *Polydora ciliata* feeds both as “Strudler” and as “Taster” (LINKE l. c.).

Lamellibranchia.—*Mytilus edulis*, *Cardium edule*, and *Mya arenaria* are typical “Strudler”, while *Macoma baltica* and *Scrobicularia plana* are intermediate between “Strudler” and “Taster”, as they search the bottom with their siphons for food (BLEGVAD l. c., THAMDRUP l. c.).

Gastropoda.—*Littorina littorea* and *Hydrobia ulvae* are both sorting deposit feeders, feeding on bottom diatoms and perhaps *Cyanophyceae* (THAMDRUP l. c., LINKE l. c.).

Crustacea.—The *Balanus* species are typical "Filtrierer". *Corophium volutator*, according to THAMDRUP (l. c.) is both "Taster" and "Filtrierer". *Crangon vulgaris* is omnivorous, and *Carcinus maenas* and *Mysis flexuosa* are preys (as to these three species, see the next chapter).

Echinoderma.—*Asterias rubens* is a preyer (see the next chapter).

THAMDRUP (l. c.) shows that the different feeding types depend on the condition of water-covering of the waddens. As regards their food uptake the suspension feeders depend on the period of water-covering, the "Taster" require only a small degree of water-covering in the form of pools, while the bottom feeders require only a certain moisture of the bottom.

B. Sources of nutrition.

Ever since the classical studies of the organic production which were carried out by VICTOR HENSEN at the end of the last century and were continued by his collaborators well into the present century (the "Kiel school"), it has been generally held that the phytoplankton is the only important original source of nutrition in the sea. Later C. G. JOHNS. PETERSEN and his collaborators (the "Petersen school") on the basis of researches carried on in the inner Danish waters, arrived at the conclusion that in enclosed shallow waters like the Danish waters it is the detritus derived from the benthos vegetation (notably the rich *Zostera* growths) which constitutes the most important source of nutrition of the bottom animals (PETERSEN and BOYSEN-JENSEN 1911, BOYSEN-JENSEN 1914, BLEGVAD 1914). However, in recent years this theory of detritus has, owing to fresh experience, receded into the background in favour of the plankton theory. The investigations of the metabolism of the phytoplankton carried out by STEEMANN NIELSEN (1937 and 1940) in the Danish waters support the view that it is the phytoplankton which is the most important food producer, and the experiments recorded below carried out by WERNSTEDT (1943), show that the detritus can hardly be considered to have any value as food for the Lamellibranchs examined by him.

Considering the conditions in the Waddensea, especially on the waddens themselves, we shall find that special conditions prevail there. As the wadden bottom is exposed to intense radiation from the sun, a rich flora of bottom diatoms will develop here, which would seem to be the chief source of nutrition for both deposit feeders and suspension feeders. THAMDRUP (1935) already regarded the bottom diatoms as an important source of food, and later investigations decidedly suggest that the bottom diatoms are by far the most important producer of nutritive substances within the area, while the phytoplankton is of secondary importance. This view is based on the investigations recorded below.

JUL. GRØNTVED, with the Skalling Laboratory as a base, has studied the phytoplankton and bottom diatom flora of the Waddensea; of these, his studies on the production of organic matter by the bottom diatoms have not yet been published. These investigations have shown that the bottom diatoms, besides occurring in great quantities on the waddens, also suspended in the water constitute an essential component of the phytoplankton. In a publication on the phytoplankton GRØNTVED (1949, p. 40) states that on a wadden with a sand bottom (off Sædding north of Esbjerg) the following numbers of bottom diatoms per cm² were found: July 1942: 105,000, August 1942: 168,000, October 1942: 66,000, November 1942: 50,000, January 1943: 67,000, February 1943: 59,000, and March 1943: 187,000. Even larger numbers were

found by BROCKMANN (1935, p. 61) and LINKE (1939, p. 270) in the German Waddensea. GRØNTVED writes that the bottom diatoms are densely concentrated in the wadden bottom down to a depth of ca. 1 cm. Further he states (l. c. p. 41) the numbers of diatoms found in the plankton samples from several stations, and it appears from them that at the various stations the bottom diatoms constitute from 15 to 62 per cent. of the numbers of diatoms registered. The two stations at which the highest percentages (48 and 62 per cent.) were found were located in the inner Waddensea in places with shallow water. It must be assumed that the suspended bottom diatoms play an even more conspicuous part over the waddens when these are flooded by water.

To acquire some knowledge of the value of diatoms as a food element, WERNSTEDT (1943), at the Skalling Laboratory, made a series of feeding experiments with young *Macoma baltica* and *Cardium edule* from the waddens. Various food elements were used: diatom cultures (*Nitzschia closterium*), cultures of *Chlorella spärcki*, and natural food elements from the wadden bottom (both rich and poor in diatoms), and for each series of experiments the growth was determined by measurement of the shells. It turned out that diatoms are valuable food elements, while detritus is of little value (though it cannot be definitely shown that it was entirely without value).

It has already been mentioned that such an important species as *Hydrobia ulvae* feeds largely on diatoms. Further we may assume that the indiscriminate bottom feeders, too, live largely on diatoms. In accordance herewith WELLS (1945) shows that *Arenicola marina* as a rule devours sinking surface sand, though in some cases it eats deeper-lying sand also.

Considering the microfauna it would seem that the *Harpacticoidea*, a group of such great importance in regard to the animal production, thrive well on diatom food. NICHOLS (1935) observed *Longipedia scotti* and *minor* eat diatoms, and the development of *L. scotti* proved to be accelerated if diatoms were added to the *Copepodit* stages. FRASER (1936) states that *Tigriopus fulvus*, which was fed with *Nitzschia closterium*, lived 3—9 months and multiplied rapidly, but died when the addition of diatoms was stopped.

The question as to the importance of sources of food other than the diatoms in the Waddensea, cannot be answered at present. A number of plankton organisms (both phyto- and zooplanktonic organisms) will, no doubt, be eaten by the suspension feeders. Attention should further be directed towards the various unicellular organisms that live on the bottom, notably the bacteria, whereas the detritus can probably be disregarded as a direct source of nutrition.

As regards the plankton organisms as food elements, it is of interest that investigations on *Mytilus californianus* (BULEY, in FOX 1936, pp. 19—27) seem to show that it is capable of selecting dinoflagellates when it takes in food from a water mass in which diatoms are highly predominant. Further LOOSANOFF (1949) states that feeding *Ostrea* are capable of choosing between different flagellates. If this selection in the intake of food is confirmed for these and for other species of bottom animals by further investigations, it will greatly complicate the estimation of the nutritive importance of the different organisms in a plankton stock.

As to bacteria, ZOBELL (1946) writes, on the basis of his own observations and facts recorded in the literature, that they may be utilised as food by various *Protozoa*, *Rotatoria*, *Copepoda*, and larger bottom animals (e. g. *Mytilus*). Whether the bacteria are of importance as a food element in the Waddensea, is unknown, no investigations being available; but it is reported by GRØNTVED (verbal information) that a rich bacterial flora is present on the waddens. ZOBELL (l. c., p. 77) states that there is a close correlation between the bacterial flora and

the diatom flora, the diatoms being of importance for bacteria both as a source of food and as a substratum, and it is mentioned that (according to GRAN 1933) the quantity of bacteria present in sea-water increases and decreases with the quantity of diatoms. The investigations made by MARE (1942) likewise suggest that the bacteria are of importance in the food cycle.

Although the information about the different sources of nutrition that can be given here is rather fragmentary, notably as regards other sources of food than the diatoms, the bottom diatoms may be regarded as the main source of nutrition for the bottom animal population of the waddens, and accordingly, indirectly, for its consumers, which will be treated in the next chapter.

It should be added that the food requirements of the bottom fauna of the waddens must be assumed to be comparatively great, both because the macrofauna consists in the main of many and relatively small individuals, and because the microfauna constitutes such a considerable part of the fauna, at any rate in the early summer. In this connection ZEUTHEN (1947) mentions that the respiration of the microfaunal organisms is 4—5 times as intense as that of the larger sea animals, whose volume is 10^4 — 10^5 times as great. This ratio corresponds to the ratio between a moderately-sized Nematode and a moderately-sized *Scoloplos armiger*.

X. Consumers of the Bottom Fauna.

In 1940 examinations of the stomach contents and intestinal contents of the plaice of the Waddensea were started at the Marine Biological Laboratory. These examinations of the food were begun by ERIK BERTELSEN, and since 1945 the present author has taken part in them. The author has also examined the stomach contents of various other consumers of the bottom fauna in order to elucidate which of them are of importance as competitors for the plaice growing up in the Waddensea. Finally, these investigations have been supplemented by data from the literature.

A. Examinations of the stomach and intestinal contents.

1) INVERTEBRATES.

Crangon vulgaris.

According to the literature, *Crangon* is omnivorous, but prefers animal food. A very comprehensive investigation, carried out by PLAGMANN (1939), of the stomach contents of 2000 individuals from the mouth of the river Elbe gave the following result: 1) The main food was constituted by *Amphipoda* (*Gammarus*, *Bathyporeia*, *Corophium*), *Polychaeta*, *Oligochaeta*, *Schizopoda*, *Lamellibranchia* (i. a. larvae), *Copepoda* (i. a. *Harpacticoidea*), *Gastropoda*, and the *Cypris* stage of *Balanus*. 2) Secondary food: *Chlorophyceae* and other plant parts, fish remains, remains of *Balanus*, *Nematodes*, insect parts, *Ostracoda*, *Cumacea*, *Nauplia* of *Balanus*, *Hydroidea* fragments. 3) Bottom material, *Foraminifera*, diatoms, etc.

In the Danish Waddensea the author examined a material of 29 individuals of varying size collected on $^{14-15}_{10}$ 1947, eight of which had empty stomachs. The other stomachs were found to contain larger or smaller quantities of bottom material kneaded together with debris of bottom animals (*Polychaeta* bristles, jaws of *Nereis*, crushed shells of *Hydrobia*, small *Lamellibranchs*, and indeterminable Crustacean remains). Stomach contents examined by

JUL. GRØNTVED were found to contain a very few diatoms; one stomach contained fairly considerable quantities of the Cyanophyce *Mereismopedia*.

***Carcinus maenas*.**

In the Waddensea *Carcinus*, which is a voracious preyer, seems largely to devour Decapods (*Crangon*, *Mysis*, and specimens of its own species). Fifty-seven individuals collected in the Waddensea on $^{10-15}/_6$ 1948 were examined for their stomach contents. Seven stomachs were empty; of the others, 48 contained remains of Decapods, five contained remains of *Hydroidia*, one contained remains of young Lamellibranchs, and one contained algal remains.

***Eupagurus bernhardus*.**

This species must likewise be regarded as a rather important consumer of the bottom fauna in the channels; but no investigations on this species are available from the Waddensea.

***Mysis flexuosa*.**

No stomach examinations were made in the Waddensea; but according to BLEGVAD (1914 and 1921) it must be assumed that *Mysis* feeds on several micro-animals of the bottom, notably *Harpacticoidea*, besides, probably, a number of plankton organisms.

***Asterias rubens*.**

No examinations were made in the Waddensea, but as the species is known from the literature to be a voracious preyer, it will, where present in fairly large numbers, no doubt consume a substantial quantity of other bottom animals.

2) PISCES.

***Centronotus gunellus*.**

Six individuals caught in the young plaice trawl on $^{14}/_{10}$ 1947 were examined as to their stomach contents. One stomach was empty, while the others contained varying quantities of *Gammarus* and *Mysis*.

***Cottus scorpius*.**

Eight individuals caught on $^{14-15}/_{10}$ 1947 had mainly *Crangon* in their stomachs, but also some *Carcinus* juv., and in one stomach the remains of a *Solea* ca. 7 cm long were found. This is in accordance with investigations carried out by BLEGVAD (1916), which show that *C. scorpius* feeds on *Crustacea* and fish.

***Gadus callarius* juv.**

The stomach contents of 16 individuals 7—10 cm long, caught on $^{15}/_{10}$ 1947, were examined. One stomach was empty, the others contained: 28 *Mysis*, 19 *Crangon*, 8 *Gammarus*, and 1 *Carcinus* juv.

***Zoarces viviparus*.**

Thirteen individuals 8—10 cm long, caught on $^{14-15}/_{10}$ for stomach examination, all contained remnants of *Gammarus*; further, one *Idothea* and one *Jaera* were found. BLEGVAD (1916) characterises the species as a Crustacean-, Lamellibranch-, and snail-feeder, and states that in fjords and coastal waters it especially eats small *Gammaridae* and *Idothea* (which con-

stituted nearly half of the stomach contents); this latter statement is in accordance with the conditions in the Waddensea.

Gobius minutus.

The stomach contents of a total of 112 individuals were examined, 45 per cent. of which had empty stomachs. Of 46 individuals collected on $^{14-15}/_{10}$ 1947, 17 had empty stomachs, while 26 contained various Crustacean remains (*Mysis*, *Crangon* juv., *Gammarus*, and *Idothea*), and the smallest three contained exclusively *Harpacticoidea* (50—100 per stomach). On $^{11}/_6$ 1946 66 individuals were collected for investigation of stomach contents and, for some of them, of intestinal contents. They were sorted into size groups, and of the individuals less than 5 cm long (20 individuals) 10 per cent. had empty stomachs, of those between 5 and 7 cm long (31 individuals) 65 per cent. had empty stomachs, and of those more than 7 cm long 100 per cent. had empty stomachs. Almost all stomachs and intestines with contents contained predominantly *Harpacticoidea*, and in addition some few Amphipod remains and some indeterminable Crustacean remains as well as undetermined eggs. In one of the largest individuals the vertebral column of a small fish (probably a small *Gobius*) was found.

To sum up, it can be said about *G. minor* in the Waddensea that it feeds primarily on young Crustaceans. At the beginning of the summer it feeds almost exclusively on *Harpacticoidea*, but later in the year it devours various other Crustacea (*Mysis*, *Crangon*, *Amphipoda*, etc.). Occasionally the larger individuals may also devour smaller fish (of their own species). These food studies show good agreement with the investigations on the food of species of the genus *Gobius* carried out by BLEGVAD (1916) in the inner Danish waters.

Limanda limanda.

Twenty-one young individuals (between 4 and 7 cm long) were caught on $^{14}/_6$ 1947 for examination of their stomach and intestinal contents. Of these, seven had empty stomachs. The individuals less than 5 cm long mainly contained *Harpacticoidea* in their stomachs and intestines (ca. 10—100 *Harpacticoidea* per stomach with contents), but in addition a few *Nereis* juv. and *Mytilus* juv. were found in the stomachs, and in the intestines some newly settled *Mya* and *Mytilus*. Individuals from 5 to 7 cm long contained, in their stomachs and intestines, fragments of *Hydroidea*, remnants of *Balanus*, a few *Crangon* juv., and a number of newly settled *Mytilus*. Thus it would seem that the smallest bottom stages feed on the microfauna of the bottom, while the somewhat larger stages in some degree feed on small epifaunal animals. Investigations made in the inner Danish waters (BLEGVAD 1916) show that *Limanda limanda* feeds primarily on the same bottom animals as the plaice, so it must be regarded as an important food competitor of the plaice.

Pleuronectes flesus.

The stomach and intestinal contents of 21 individuals from the interior of Ho Bay were examined in 1947. Seven of them had empty stomachs. Twelve individuals fished about the middle of August contained *Crangon* juv. and *Corophium* (the stomachs contained ca. 60 per cent. of *Crangon* and ca. 10 per cent. of *Corophium*). Nine individuals caught in October contained *Crangon* juv., *Corophium* (a single specimen in an intestine), *Pygospio*, and the posterior part of an *Arenicola*.

Investigations made by BLEGVAD (1916) in the inner Danish waters showed that *P. flesus* consumed the same bottom animals as the plaice, so it must be regarded as a food competitor of the latter.

Pleuronectes platessa.

In the years 1940—47 the stomach and intestinal contents of the following numbers of plaice were examined:

	0-group	I—III groups
1940	416	291
1941	333	281
1942	89	555
1943	210	555
1944	20	60
1945	278	465
1946	..	223
1947	116	175
Total...	1,462	2,605

Of the 1,462 0-group plaice 24 per cent. had empty stomachs, and of the 2,605 older individuals 52 per cent. had empty stomachs. The examination of the food constituents was based on examinations of both stomach and intestinal contents, but in the estimation of the quantitative composition only the stomach contents were taken into consideration, as easily digestible food elements cannot be recognised, or can only be recognised with difficulty, in the intestinal contents. The following food elements were found:

Polychaeta: *Phyllodocidae*, *Nereis*, *Nephtys*, *Pygospio*, *Arenicola* (mostly bitten-off hind parts), *Capitellidae*, *Scoloplos*, *Pectinaria*.—*Oligochaeta*.—*Nematodes*.—*Lamellibranchia*: 0-group individuals of *Cardium*, *Macoma*, *Mya*, *Mytilus*, and *Spisula*?—*Gastropoda*: *Hydrobia*, *Retusa*.—*Crustacea*: *Ostracoda*, *Harpacticoidea*, *Corophium*, *Gammarus*, *Cumacea*, *Mysis*, *Crangon*, *Carcinus* juv.—*Pisces*: *Clupea* sp. juv.

As there is a difference between the food of 0-group plaice and that of older groups of plaice, they will be treated separately.

At the beginning of the summer (before attaining a length of ca. 5 cm) the 0-group plaice feed primarily on very small Crustaceans. In most places the *Harpacticoidea* constitute the main food, and in many cases the only food element. Besides, small numbers of *Ostracoda* sometimes occur. In localities in which *Corophium volutator* is present in considerable quantities, young individuals of this species seem to be preferred as food, as was the case in some years in the interior of Ho Bay (see below). In addition to these small Crustaceans, small *Polychaeta* (*Pygospio*) and *Oligochaeta* as well as diminutive newly settled Lamellibranchs may sometimes be found. Later in the season, when the 0-group individuals have grown larger, the food is more variable, and the *Harpacticoidea* and the *Ostracoda* are of no importance as food. According to the composition of the bottom fauna the following food elements will be of importance: *Corophium*, *Mysis*, *Crangon* juv., various small *Polychaeta*, bitten-off hind parts of *Arenicola*, *Oligochaeta*, 0-group *Lamellibranchia*, and *Hydrobia*. On rare occasions a number of *Nematodes* were found in the stomachs, but probably they are only eaten in the absence of suitable food, and probably they are of little or no nutritive value, as they may be found undigested even in the hindmost part of the intestine. Thus it will be seen that while the smallest 0-group plaice feed exclusively on the microfaunal animals of the bottom, the food of the 0-group later in the season exhibits almost the same composition as that of the older age-groups.

The food of the older age-groups is rather varied. Of the *Polychaeta* the most important are *Arenicola* and *Scoloplos*. Of *Arenicola* in most cases only the posterior parts are taken; these bitten-off fragments are frequently found mixed with the stomach contents, but whole individuals of a smaller size may occur, also. Further, *Nereis* and *Nephtys* are of importance, while *Pygospio* hardly plays any role for the larger plaice. Of the Lamellibranchs, 0-group individuals of *Cardium*, *Macoma*, and *Mya* constitute the chief food, but *Mytilus*, also, may occur. Of the snails, *Hydrobia* is a frequent constituent of the stomach and intestinal contents, whereas *Littorina* has not yet been observed in the stomach and accordingly cannot be of great importance, though it is probable that some 0-group *Littorina* are occasionally devoured. The most important Crustacea are *Corophium*, *Mysis*, and *Crangon*, while *Carcinus* juv., *Gammarus*, and *Cumacea* play a less important role. Exceptionally young *Clupea harengus* or *C. sprattus* have been found in the stomachs of large plaice. The composition of the stomach contents depends, of course, on the composition of the bottom fauna, and as this latter is subject to considerable variations in the course of the year and from one year to another, these will be reflected in the composition of the food, as will appear from the examples below:

In the summer of 1940 *Corophium* was by far the most important food element for plaice both of the 0-group and the older age-groups in the interior of Ho Bay (for the 0-group *Corophium* constituted 100 % of the food in June, ca. 55 % in September and ca. 40 % in October; for the older plaice *Corophium* constituted 75–100 % in June, but in September and October only a negligible part). In 1941 *Corophium* was only sparsely represented in the stomach samples from Ho Bay derived from both 0-group and older plaice. In 1942 *Corophium* was found here and there in fairly large quantities in the stomach samples, but never in such great numbers as in 1940. In 1943 *Corophium* was again the most important food element in Ho Bay for plaice less than 10 cm long, and for the larger plaice it was a fairly essential food element. From 1944 no data and from 1945 only insufficient data are available from Ho Bay. In 1946 *Corophium* seems to have been the dominant food element in April and June (0-group plaice not found); from the latter part of the season no investigations of the food are on record. In 1947 *Corophium* in the interior of Ho Bay constituted by far the most important food of both 0-group and older plaice in June, but later (in August and October) other food elements dominated; even as late as August *Corophium* still formed a substantial part of the food, especially for the 0-group.

As for the Lamellibranchs similar fluctuations occur in their importance as a food element. Thus numerous *Cardium* were found in the stomachs of big plaice in 1940, while in 1941 they were only sparsely present. In 1942 the settling and growth of *Cardium* brood was exceptionally lively, and in the same year 0-group *Cardium* constituted a much greater part of the food than in the two previous years. At first they occurred as quite small individuals in the stomachs of the smallest plaice in June, but in August and September they constituted ca. 75 % of the food of the older plaice. 1945, again, was a year with a rich *Cardium* brood, and in August of that year *Cardium* was the dominant food element for larger plaice. In 1947 many 0-group *Cardium* occurred, but as the 0-group of *Mya*, which was the preferred food element, was even more numerous, it was not till late in the season (October) that *Cardium* became of importance as food. In addition Polychaetes (especially the hind parts of *Arenicola*) constituted an essential food element that year.

It will be seen from these examples that as a rule the food elements which are most abundant constitute the main part of the stomach contents (*Corophium* in Ho Bay, *Cardium* 0-group on the sand waddens), but it will also be seen that out of several food elements occur-

ring in quantity the plaice may prefer one, as was the case in 1947, when they preferred *Mya* to *Cardium*.

Owing to their abundance, the plaice must be regarded as the chief consumer of the bottom fauna of the waddens and accordingly as the primary cause of its decimation in the summer half-year. Such a decimation is especially found within the 0-groups of Lamelli-branches, *Hydrobia*, and some Polychaetes. Particularly instructive in this respect are the numbers of 0-group *Cardium edule* and *Mya arenaria* per m² of wadden in the 1947 season (table 7).

Table 7.

Sand wadden north of Fano			Sand wadden northeast of Fano			Soft wadden at Nordby		
Date	<i>Cardium</i>	<i>Mya</i>	Date	<i>Cardium</i>	<i>Mya</i>	Date	<i>Cardium</i>	<i>Mya</i>
18/6	2,200	30,000	22/6	6,100	3,500	22/6	16,500	43,000
22/7	2,000	11,800	20/7	7,700	3,300	20/7	7,400	26,000
29/8	ca. 800	9,400	28/8	4,200	200	28/8	5,200	11,600
10/10	1,100	ca. 130	9/10	1,400	ca. 10	8/10	0	ca. 10
30/10	850	ca. 100	30/10	550	0	30/10	0	0

It appears distinctly from this table that the population of 0-group *Mya* was more numerous than the population of 0-group *Cardium* at the beginning of the season. But since *Mya*, as mentioned above, was the most vigorously pursued, the brood of this species was almost exterminated, while a limited part of the brood of *Cardium* had a possibility of surviving. As the succeeding winters (1947—48 and 1948—49) were mild, there was an abundant population of *Cardium* from the year 1947 in the summers of 1948 and 1949. For comparison we may consider the 0-group of 1942, which, as mentioned above, was exceptionally numerous; it was not accompanied by a rich population of 0-group *Mya*, the consequence of which was

Table 8.

1940			1941			1942			1943		
Date	% empty		Date	% empty		Date	% empty		Date	% empty	
	0-group	older		0-group	older		0-group	older		0-group	older
			18-20/6	0	28	28/6-1/7	..	28	30/6-4/7	0	39
			20-23/8	23	29	11-13/8	0	31			
6/9-12/9	14	35				9-19/9	17	30	16-22/9	2	44
29/10-2/11	53	94	28/10-2/11	34	52	28-30/10	30	73	30/10-8/11	83	89

1944			1945			1947		
Date	% empty		Date	% empty		Date	% empty	
	0-group	older		0-group	older		0-group	older
			27/6-7/7	0	80	14-16/6	0	34
			28/8-3/9	43	72	13/8	42	48
22/11	95	90	30/10-4/11	62	91	7-15/10	50	45

that the young *Cardium* were subject to such an intense pursuit that they were practically exterminated in the course of the same season, so no stock of importance of the year-group 1942 was found in the succeeding years.

At various times of the year the percentage quantity of empty stomachs was studied (see table 8). This table shows that the number of empty stomachs increases in the course of the season, the stomach contents at the end of the season being negligible. Further, it will be seen that the number of empty stomachs is lowest for the 0-group and highest for the older age-groups. The intake of food is accordingly most intense at the beginning of the season, and the young plaice feed more heavily than the older ones.

It has further turned out that in summer, when the feeding takes place, a smaller number of empty stomachs will be found in the interior of Ho Bay than in the other localities—at any rate in the I—III-groups. The explanation of this is to be found in the fact that in the inner shallow-watered Ho Bay the bottom is everywhere rich in food elements, so the plaice can constantly take in food, while the other fishing stations border on the deeper channels poor in food, in which an essential part of the fish stock stays during the low-water period. In a single case (September 1940) the same proportion was found for the 0-group (see table 9).

Table 9.

Year and date	Age-group	Locality	Number of stomachs	Percentage of empty stomachs
1940 6-12/9	0-gr.	Inner Ho Bay.....	43	0
		E. of Langli Sand.....	78	3
		N. of Fanø and N. of Esbjerg harbour....	55	18
1941 18-20/6	I—III-gr.	Inner Ho Bay.....	50	ca. 10
		E. of Langli Sand.....	40	60
		N. and NE. of Fanø and N. of Esbjerg harbour	97	27
1942 28/6-1/7	I—III-gr.	Inner Ho Bay.....	93	17
		E. of Langli Sand.....	90	21
		NE. of Fanø and N. of Esbjerg harbour ...	75	24
1942 11 13/8	I—III-gr.	Inner Ho Bay.....	20	15
		E. of Langli Sand.....	25	44
1942 9-12/9	I—III-gr.	Inner Ho Bay.....	35	20
		E. of Langli Sand.....	30	50
1943 20/6-4/7	I—III-gr.	Inner Ho Bay.....	50	30
		E. of Langli Sand.....	55	60
		N. of Esbjerg harbour	30	67
1946 20/6	I—III-gr.	Inner Ho Bay.....	22	32
		N. of Fanø	25	80
1947 14-16/6	I—III-gr.	Inner Ho Bay.....	30	10
		E. of Langli Sand	40	50
		NE. of Fanø and N. of Esbjerg harbour ...	33	55

3) BIRDS.

At the times of migration, especially in the late summer and autumn, large flocks of birds are encountered on the waddens, where they feed on small animals. These bird flocks may, no doubt, contribute greatly to the decimation of minor bottom animals such as *Corophium*, *Hydrobia*, small *Littorina*, various *Polychaeta*, and small 0-group *Lamellibranchia*.

B. Summary and discussion.

When at the beginning of the summer (as a rule in June) the 0-group plaice migrate into the Waddensea, the great majority are less than 5 cm long, and their food is the microfauna of the wadden bottom (mainly *Harpacticoidea*, but also *Ostracoda*, *Corophium* brood, etc.). Later in the season the food of the 0-group, like that of the older plaice, consists of various smaller infauna animals.

During their growth the plaice have several food competitors. Mention should first be made of their near relatives *Pleuronectes flesus*, *Limanda limanda*, and *Solea solea*, which feed in the same way as the plaice. Of these, *Limanda limanda*, which far exceeds the other two in number, though it is less numerous than the plaice, is of the greatest importance.

Gobius minutus, *Crangon vulgaris*, *Mysis flexuosa*, and *Carcinus maenas* must be assumed to be competitors, also, owing to their great abundance. It is especially to the 0-group that they are serious competitors, for they chiefly consume the microfauna and the smaller animals of the macrofauna. The first-mentioned three will be the most important competitors, as they may migrate on a large scale with the flood water in over the waddens, while *Carcinus* is more closely associated with the channels. Thus *Crangon* and *Mysis* are of importance both as consumers and as producers of fish food.

Like *Carcinus*, *Eupagurus bernhardus* and *Asterias rubens* must be regarded as considerable consumers of bottom animals in the channels in the places where they are most numerous.

The species of Pisces that are not so definitely associated with the bottom as the flatfish (*Centronotus gunellus*, *Gadus callarias* juv., *Cottus scorpius*, *Zoarces viviparus*) feed predominantly on free-living Crustaceans (*Mysis*, *Crangon*, *Gammarus*, *Carcinus* juv.), whereas the infauna of the bottom is hardly of great significance as food for them. These fish, therefore, are of less importance as food competitors for the plaice than those mentioned above.

Finally, a certain importance as food competitors must be ascribed to the large flocks of migrating birds.

XI. The Quantitative Conditions of the Bottom Fauna, with special reference to the young-plaice food.

Quantitative investigations of the bottom fauna were made with the special object of determining the quantity of food available for the young flatfish (notably plaice), that is to say, the bottom animals which serve as food for the youngest age-groups (the 0-, I-, II-, and possibly the III-group) of these species of fish. On the basis of the examinations of the stomach contents recorded in the preceding chapter, the following bottom animals can be characterised as food animals for young plaice:

1) The microfauna of the bottom.

a) Actual microfauna: The *Harpacticoidea* and the *Ostracoda* are important food elements, especially the former, owing to their much greater abundance. *Nematodes* and *Foraminifera*, however, seem to be of little or no significance as food for fish.

- b) The brood of the macrofauna: *Polychaeta*, *Hydrobia ulvae*, and *Lamellibranchia*.
 2) The macrofauna of the bottom.

Polychaeta and *Oligochaeta*: All the species are valuable food animals, provided they are not so deeply buried in the bottom that they avoid capture. As to *Arenicola marina*, the greater part of the animal is so deeply buried in the bottom that only the posterior parts are accessible to the fish; hence, only the posterior parts (average weight ca. 0.06 g) have been regarded as constituting part of the food of young fish.

Gastropoda: Owing to its abundance *Hydrobia ulvae* is an important food element, and in addition *Retusa obtusa*, where present, is a favourite food. *Littorina littorea* was not observed in the stomachs, but it is quite likely that young individuals are devoured now and then.

Lamellibranchia: The 0-group of *Cardium edule*, *Macoma baltica*, *Mya arenaria*, and *Mytilus edulis*, and perhaps the I-group of *Macoma baltica* may be included in the food of young fish, but not the older age-groups, as they seem to be of no value.

Crustacea: *Corophium volutator*, *Bathyporeia pilosa*, *Gammarus* sp., and the 0-group of *Crangon vulgaris* are favourite food animals, and in addition a number of the smaller *Carcinus maenas* of the 0-group are devoured. *Mysis flexuosa*, which is an important food animal, was very rarely present in the bottom samples, since, to a much greater extent than *Crangon*, it leads a free life above the bottom.

The methods employed in the quantitative collecting and in counting and weighing the bottom animals have been described in chapter II (pp. 5—7). In the following pages the bottom fauna on the waddens and in the channels will be treated separately.

A. Waddens.

1) Investigations in the southern part of the Danish Waddensea in 1941.—During a comprehensive hydrographic, geological, and biological investigation of the Danish Waddensea in the summer of 1941, a number of quantitative collections of the bottom fauna on the waddens and in the channels were carried out under the leadership of H. M. THAMDRUP in the period from July 18 to August 31. The working up of the material collected was entrusted to the author of the present work. The collections were made along several sampling lines, as shown in the map in fig. 40. A total of 303 bottom samples were secured, but of these only 211 were suitable for an estimation of the quantity of the fauna, while the remaining samples were only used to illustrate the occurrence of the species. Of the 211 samples, 201 were derived from wadden areas (167 of $\frac{1}{100}$ m² and 34 of $\frac{1}{20}$ m²). The sampling was very scattered, rarely more than one or perhaps two samples being taken at each station. Hence a more detailed description of the quantitative distribution of the species was not possible, so a more summary treatment of the material was necessary. Each sampling line was divided according to the quality of the bottom, in some cases according to level, and for each section of the line the average values of the total quantities of animals per areal unit (number of individuals and weight in grammes per m²) and the average values for the food of young plaice (number of individuals, gross weight and live weight per m²) were ascertained. The live weight is the gross weight less the weight of calcareous shells of shell-bearing Mollusca.

The total result is given in the subjoined survey, which indicates minimum, maximum, and average values for the whole area investigated:

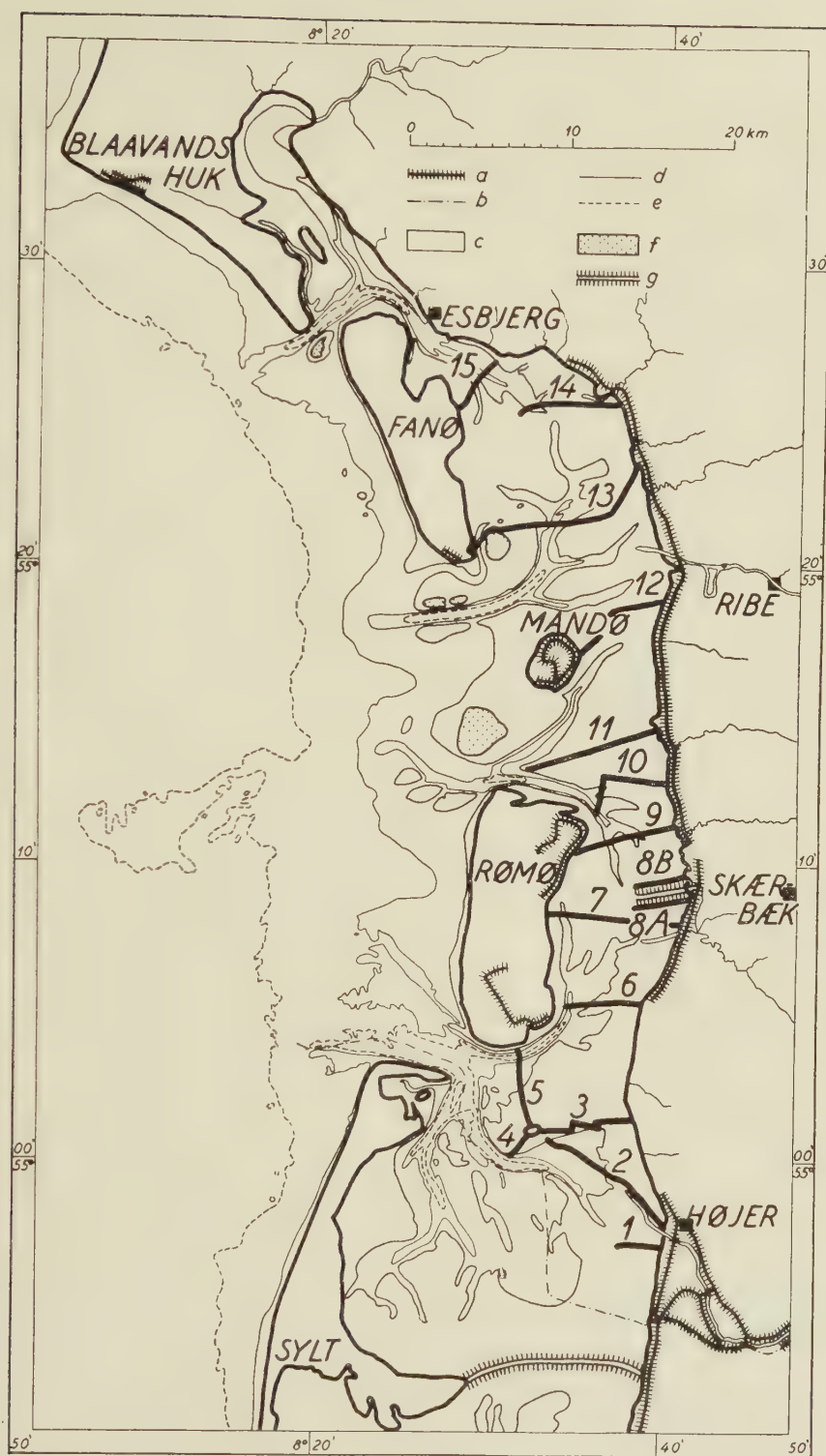


Fig. 40. Sampling lines in the southern part of the Waddensea in 1941.



Fig. 41. Map of the northern part of the Danish Waddensea showing stations for bottom sampling in the channels in 1942 (A, B, C, D, E, H), stations for dredging in 1942—43 (black squares), collecting stations on the sand wadden northeast of Fanø and on the soft wadden at Nordby on Fanø (black triangles), and sampling lines on the waddens at Skallingen (I and II) and north of Fanø (III).

		Minimum	Average	Maximum
Total	individuals per m ²	7,000	31,000	74,650
	gross weight per m ²	15 g	174 g	623 g
Food of young plaice	individuals per m ²	6,800	30,890	74,630
	gross weight per m ²	15 g	84 g	200 g
	live weight per m ²	10 g	39 g	80 g

From these figures it appears that there is a very small difference between the total numbers of individuals and the numbers of food animals for the young fish, whereas the average weight of food animals is hardly half the average of the total weight. It will likewise be seen that the nutritive value of the waddens (the live weight of food animals for young plaice) varies much less than the total gross weights.

2) Investigations north of Fano in 1946, 1947, and 1949.—On the sand wadden north of Fano and on the soft wadden off Nordby more detailed investigations were carried out, samples both of the microfauna and of the macrofauna being collected at different times of the season. The results of these investigations are given in tables 10—17. If the total number of animals counted was low (<10), the figure is given in parenthesis, and in such cases the quantities computed must be accepted with reserve; an *r* indicates very few individuals.

On the sand wadden north of Fano the collections were made along a sampling line ca. 450 m long extending from the edge of the wadden to the shore, i. e. the high-water mark (see the map in fig. 40). For most of the collections four sampling stations were selected, and the distance between these was measured by counting our steps when walking over the wadden. In the tables the position of the stations is indicated by the distance in metres from the edge of the wadden. The results of the various collections are as follows:

1946.—Collections were made on June 22—26 (17 micro-samples of 0.95 cm², 16 skimmer-samples of 25 m², 54 macro-samples of $\frac{1}{100}$ m² (13 of these were only examined for Lamellibranchs), 14 macro-samples of $\frac{1}{20}$ m² examined for Lamellibranchs) and on October 15—16 (20 micro-samples of 0.95 cm², 16 skimmer-samples of 25 cm², and 70 macro-samples of $\frac{1}{100}$ m², 40 of which were only examined for Lamellibranchs).

In the June-samples the microfauna presents a fairly considerable weight of food for young plaice over the greater part of the wadden (between 10 and 12 g per m²), low weights being found only nearest the shore (ca. 2 g per m²). On the outermost part of the wadden the actual microfauna constitutes the greatest quantity by weight, while at the other stations the weight is equally distributed between the true microfauna and the brood of the macrofauna. The weight of the macrofauna in the June samples as regards food for young plaice is comparatively low on the outer half of the wadden (8—20 g per m², or only little more than the microfauna), and here *Scoloplos* constitutes the main part. On the inner part of the wadden the quantity of food for young plaice is much larger (between 108 and 139 g per m²) owing to a fairly numerous population of *Hydrobia ulvae*. In the October samples the microfauna (the true microfauna as well as the brood of the macrofauna (combined less than 1 g per m²)) represents only negligible weights of fish food. However, over the greater part of the wadden (with the exception of the outermost station) the October samples contain much larger quantities of young-plaice food of the macrofauna than the June samples (viz. ca. 119—ca. 377 g per m²). This great increase is chiefly due to the production of a numerous 0-group of *Hydrobia ulvae*.

Table 10. Microfauna of the bottom

Distance from low-water mark	22 June 1946					
	0-10 m		ca. 150 m		ca. 350 m	
Number and weight (g) per m ²	N	W	N	W	N	W
<i>Harpacticoidea</i>	837,000	8.3	534,000	5.3	455,000	4.8
<i>Ostracoda</i>	24,000	0.3	15,000	0.2	2,000	<0.1
<i>Cumacea</i>	(100)	..	(600)	..	..	..
<i>Nematodes</i>	1,048,000	5.2	708,000	3.5	287,000	1.4
<i>Hydrobia ulvae</i> 0-group.....	8,600	0.1	27,000	0.9	88,000	0.3
<i>Cardium edule</i> -	7,000	0.6	22,000	1.8	2,500	0.2
<i>Macoma baltica</i> -	(900)	(0.4)	(700)	(0.2)	5,900	1.2
<i>Mya arenaria</i> -	..	..	..	..	..	..
<i>Mytilus edulis</i> -	..	..	(100)	(<0.1)	..	..
<i>Nephtys hombergi</i> -	(300)	(<0.1)	1,000	<0.1	..	..
<i>Scoloplos armiger</i> -	(600)	(0.2)	(400)	(0.2)	11,000	4.4
<i>Pygospio elegans</i> juv.	1,800	(0.9)	32,000	1.6	..	..
<i>Bathyporeia</i> sp.....	..	..	..	..	(200)	(0.7)
Total...	ca. 1,900,000	ca. 16	ca. 1,341,000	ca. 13.5	ca. 852,000	ca. 13.5
Young-plaice food...	ca. 887,000	ca. 11	ca. 633,000	ca. 10	ca. 656,000	ca. 12

1947.—Samples collected on July 21–22 (24 micro-samples of 0.95 cm², 16 skimmer-samples of 25 cm², and 15 samples of 1/100 m²) and on October 10 (32 micro-samples of 2.25 cm² and 12 samples of 1/100 m²).

In the July samples from all parts of the wadden only small weights of young fish food of the microfauna (less than 1 g per m²) were found. The macrofauna, however, presented considerable quantities of young-plaice food (54–234 g per m²), the smallest quantities occurring on the outer part of the wadden and the largest nearest the shore. The greater part of these weights was constituted by *Hydrobia ulvae* (especially the 0-group individuals, which were the sole representatives of the species on the outer half of the wadden). At the station located 160–170 m from the edge of the wadden there occurred in addition large quantities of 0-group individuals of *Cardium* and *Mya* (16.5 g per m² and 62 g per m², respectively), which together represented a larger weight than *Hydrobia* (78 g per m²). In October, also, very small quantities of microfaunal animals were found. But—with the exception of the extreme outer station—the quantities of young plaice food of the macrofauna were even larger in October than in July (near the edge of the wadden 14 g per m², ca. 170 m nearer the shore 289 g per m², and nearest the shore 485 g per m²). At the midmost of these stations the *Cardium* 0-group constituted the greater part (ca. 205 g per m²), next came the *Hydrobia* 0-group (77 g per m²), while nearest the shore *Hydrobia* constituted by far the largest quantity (476 g per m²).

1949.—The collections, which were only made at one station (ca. 170 m from the edge of the wadden), were taken on July 1st (5 micro-samples of 2.25 cm², 4 skimmer-samples of 25 cm², and 10 macro-samples of 1/100 m²) and on September 1st (10 micro-samples of 2.25 cm², 4 skimmer-samples of 25 cm², and 10 macro-samples of 1/100 m²).

the sand wadden north of Fanø.

15—16 October 1946									
430—440 m		ca. 0—10 m		ca. 170 m		340—350 m		430—440 m	
N	W	N	W	N	W	N	W	N	W
6,000	1.2	19,000	0.19	4,000	0.04	2000	0.02	15,000	0.15
8,000	0.2	21,000	0.25	19,000	0.23	2000	0.02	3,000	0.04
..	..	r	..	..	..	..	..	..	..
4,000	0.6	42,000	0.21	33,000	0.17	16,000	0.08	88,000	0.44
(500)	(<0.1)	..	..	..	..	..	..	..	..
..	..	(400)	(0.03)	(100)	(0.01)	(100)	(0.01)	..	..
(900)	(0.2)	(500)	(0.04)	(400)	(0.03)	(100)	(0.01)	(400)	(0.03)
..	..	..	..	(700)	(0.06)	..	..	..	..
(300)	(<0.1)	..	..	..	..	(100)	(0.01)	..	..
..	..	..	..	..	..	..	..	..	..
(200)	(0.1)	..	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..
60,000	ca. 2.5	ca. 83,000	ca. 0.9	ca. 57,000	ca. ~~0.3~~ 0.5	ca. 20,000	0.1—0.2	ca. 106,000	ca. 0.7
36,000	ca. 2	ca. 41,000	ca. ~~0.7~~ 0.7	ca. 24,000	ca. ~~0.2~~ 0.3	ca. 4,000	ca. 0.1	ca. 18,000	ca. 0.2

At the sampling on July 1 conditions were about the same as were met with at the end of June 1946 in the same locality, a comparatively large quantity of young plaice food of the microfauna (between 7 and 8 g per m²) being found, but this year it consisted predominantly of true microfaunal animals, while brood of the macrofauna was only sparsely present. The macrofauna constituted only ca. 30 g per m². On September 1st the microfauna contained only between 1 and 2 g of young plaice food per m², and at the same time the quantity of food supplied by the macrofauna had not increased (only ca. 34 g per m²), which was probably due to a slight production of brood as well as to a rapid consumption of the brood produced. Besides the young-plaice food, the total macrofauna in the samples was weighed; on July 1st it amounted to 796 g per m² and on September 1st to 892 g per m²; that is to say that the macrofaunal young-plaice food at both these samplings constituted only about 3.8 per cent of the total weight of animals found. The greater part of the young-plaice food consisted of *Scoloplos armiger*. Of the total quantity of animals, the II-group of *Cardium edule* (year-group 1947) represented by far the greatest weight. That this population of *Cardium* of the II-group was of no value as food, appears from the fact that approximately the same density of individuals was observed at the two dates of sampling (450 and 480 individuals per m², respectively).

3) On the soft wadden at Nordby (see the map in fig. 41) samples were taken on August 28 and October 8, 1947, (see tables 16—17). On both these dates only inconsiderable quantities of microfaunal young plaice food were found (less than 1 g per m²). Of the macrofauna a very large quantity of young-plaice food was found in August (485 g per m²), of which the *Hydrobia ulvae* 0-group constituted the greater part, while the 0-groups of *Cardium edule* and *Mya arenaria* also occurred in quantity. In October the young-plaice food had been reduced to ca. 20 g per m², the 0-groups of *Hydrobia*, *Cardium*, and *Mya* having almost disappeared.

Table 11. Macro-fauna of the bottom

Distance from low-water mark.....	22—26 June 1946							
	ca. 0—10 m		80—90 m		ca. 170 m		ca. 230 m	
	N	W	N	W	N	W	N	W
<i>Lepidonotus squamatus</i>	..	..	..	..	..	..	..	..
<i>Phyllodoce maculata</i>	..	..	..	..	(10)	(0.3)	(20)	1 (0.5)
<i>Eteone longa</i>	(50)	(0.9)	(40)	(0.7)	(30)	(<0.1)	(40)	(<0.1)
<i>Nereis diversicolor</i> { 0-group.....	..	..	..	..	(10)	(0.1)	(60)	(0.5)
adults.....	..	..	..	..	..	..	..	..
<i>Nephtys hombergi</i> { 0-group.....	..	..	..	..	..	..	..	..
adults.....	(20)	(1.5)	..	..	(30)	(2.0)	(20)	(1.6)
<i>Scoloplos armiger</i> { 0-group.....	..	..	..	..	..	..	..	..
adults.....	220	12.3	200	12.3	(110)	(4.3)	440	16.9
<i>Capitellidae</i>	(50)	(0.2)	(50)	(0.2)	(30)	(0.1)	(80)	(0.3)
<i>Arenicola marina</i> (hind parts).....	10	0.6	7	0.4	13	0.8	13	0.8
<i>Pygospio elegans</i>	290	0.3	340	0.3	460	0.4	740	0.6
<i>Polydora</i> sp.....	..	..	..	..	..	..	..	..
<i>Magelona papillicornis</i>	(10)	(0.1)	..	..	..	..	..	..
<i>Oligochaeta</i>	..	..	..	..	(10)	(<0.1)	(20)	(<0.1)
<i>Nemertini</i>	..	..	..	..	..	..	..	..
<i>Hydrobia ulvae</i> { 0-group.....	..	..	..	..	..	..	..	..
adults.....	(<500)	(ca. 0.8)	..	..	..	..	..	..
<i>Cardium edule</i> { 0-group.....	..	..	..	..	..	..	..	..
adults.....	(10)	..	430	..	500	..	180	..
<i>Macoma baltica</i> { juv.....	(10)	(0.1)	(60)	(0.3)	(<10)	(<0.1)	(40)	(0.2)
adults.....	..	..	(20)	..	(10)	..	..	..
<i>Mya arenaria</i>	..	..	..	..	..	..	..	..
<i>Corophium volutator</i>	..	..	(20)	(<0.1)	(30)	(<0.1)	200	0.2
<i>Bathyporeia</i> sp.....	..	..	..	..	..	..	(20)	(0.1)
<i>Idothea</i> sp.....	..	..	..	..	..	..	..	..
<i>Crangon vulgaris</i> (juv. + adults).....	..	..	(20)	(0.1)	(50)	(0.2)	(60)	(0.2)
<i>Carcinus maenas</i> (juv.).....	..	..	..	..	..	..	..	..
Young-plaice food.....	ca. 1,000	ca. 17	ca. 760	ca. 14	ca. 800	ca. 8	ca. 1,750	ca. 22

NB: *Arenicola* only counted in June, but as the stock did not seem to have changed, these figures are also used for October.

Table 12. Micro-fauna of the bottom

Distance from low-water mark.....	21 July 1947					
	ca. 0—10 m		160—170 m		ca. 300 m	
	N	W	N	W	N	W
<i>Harpacticoidea</i>	(4,000)	(0.04)	(7,000)	(0.07)	(7,000)	(0.07)
<i>Ostracoda</i>	30,000	0.36	11,000	0.13	(<1,000)	(<0.01)
<i>Nematodes</i>	300,000	1.50	258,000	1.29	82,000	0.42
Total...	334,000	1.9	276,000	1.5	89,000	0.5
Young-plaice food...	34,000	0.4	18,000	0.2	7,000	ca. 0.1

the sand wadden north of Fanø.

15—16 October 1946											
ca. 320 m		430—440 m		ca. 0—10 m		ca. 170 m		ca. 340 m		430—440 m	
N	W	N	W	N	W	N	W	N	W	N	W
..	..	..	..	(10)	(<0.1)	..	..	..	..	..	..
(80)	(0.6)	(70)	(0.3)	(60)	(0.2)	(20)	(0.1)	..	..	..	..
480	0.4	2,150	1.1	..	..	..	..	(130)	(1.3)	(30)	(1.4)
..	..	(20)	?	..	..	(10)	(0.8)	(30)	(<0.1)	2,300	20.5
..	..	..	..	120	1.7	..	..	(20)	(2.0)	(200)	(20.0)
..	..	..	..	..	..	(10)	(1.1)	..	..	..	..
..	..	..	..	130	0.2	110	0.4	(20)	(0.9)	..	..
230	16.7	200	11.5	(50)	(3.7)	(90)	(5.1)	230	0.9	(30)	(0.1)
220	0.7	330	1.6	..	..	..	..	220	12.6	..	..
13	0.8	2	0.1	..	..	..	..	(20)	(0.1)	530	0.6
420	0.3	2,480	1.4	10	0.6	13	0.8	13	0.8	2	0.1
..	..	..	..	(60)	(0.1)	(30)	(<0.1)	(200)	(0.8)	2,100	8.5
..	..	..	..	..	..	..	..	..	..	(30)	(0.1)
..	..	..	..	(10)	(0.1)	..	..	..	..	..	..
850	1.1	580	0.7	..	..	..	..	(100)	(0.1)	1,800	2.1
..	..	(20)	(0.5)	..	..	..	..	..	..	..	..
..	..	..	..	r	(<0.1)	117,000	110.8	75,200	..	..	..
4,300	86.1	61,100	118.3	..	..	..	..	13,000	197.6	45,300	320.0
..	..	..	..	..	..	..	..	(90)	(11.0)	25,500	..
(90)	..	..	..	140	..	610	..	(30)	..	..	..
(10)	(1.1)	..	..	(40)	(2.6)	(10)	(<0.1)	(20)	(0.9)	(100)	(3.1)
..	..	(20)	..	(20)	..	(10)	..	(30)	..	(130)	..
..	..	(<10)	..	..	..	..	..	..	..	..	..
(70)	(0.1)	1,300	2.2	..	..	..	..	..	..	..	..
..	..	(20)	(0.1)	..	..	..	..	(50)	(0.1)	(50)	(0.1)
..	..	(80)	(0.2)	..	..	..	..	50	(0.1)	..	..
(120)	(0.4)	(80)	(0.4)	..	..	(30)	..	(30)	..	(50)	..
..	..	(20)	(<0.1)	..	..	r	..	(10)	..	(30)	..
36,800	ca. 108	ca. 68,500	ca. 139	ca. 510	ca. 9	ca. 117,000	ca. 119	ca. 89,000	ca. 229	ca. 78,000	ca. 377

the sand wadden north of Fanø.

10 October 1947									
420—430 m		0—25 m		ca. 170 m		ca. 300 m		ca. 440 m	
N	W	N	W	N	W	N	W	N	W
(2,000)	(0.02)	85,000	0.84	36,000	0.36	(600)	(0.01)	(2,000)	(0.02)
12,000	0.14	16,000	0.19	8,000	0.10	<1,000	(ca. 0.01)	(2,000)	(0.02)
18,000	0.09	75,000	0.38	82,000	0.41	71,000	0.36	43,000	0.22
32,000	0.25	176,000	ca. 1.4	126,000	ca. 0.9	ca. 72,000	ca. 0.4	ca. 47,000	ca. 0.3
14,000	0.15	ca. 101,000	ca. 1	ca. 44,000	ca. 0.5	ca. 1,000	<0.1	ca. 4,000	0.1

Table 13. Macro-fauna of the bottom

Distance from low-water mark	21—22 July 1947			
	ca. 0—10 m		160—170 m	
	N	W	N	W
Number and weight (g) per m ²				
<i>Phyllodoctidae</i>	(170)	(0.3)	(230)	(0.6)
<i>Nereis diversicolor</i> { 0-group	(70)	(0.9)	370	4.6
adults	..	..	..	..
<i>Scoloplos armiger</i> (adults)	(70)	(0.3)	270	1.1
<i>Pygospio elegans</i>	500	0.5	(130)	(0.1)
<i>Polydora</i> sp.	..	..	(70)	(0.2)
<i>Cirratulus cirratus</i>	..	..	..	..
<i>Capitellidae</i> (juv. + adults)	(70)	(0.1)	..	..
<i>Arenicola marina</i> (hind parts)	18	1.1	28	1.7
<i>Oligochaeta</i>	..	..	..	..
<i>Hydrobia ulvae</i> { 0-group	440,000	44.0	120,000	78.0
adults	..	..	..	..
<i>Cardium edule</i> 0-group	3,200	1.6	2,000	16.5
<i>Macoma baltica</i> { 0-group	600	0.6	(300)	(1.1)
adults	..	..	(200)	..
<i>Mya arenaria</i> (0-group)	8,600	5.0	11,800	62.0
<i>Corophium volutator</i>	..	..	..	..
<i>Gammarus</i> sp.	..	..	..	..
<i>Idothea</i> sp.	..	..	..	..
<i>Crangon vulgaris</i> (juv.)	..	..	(30)	(0.1)
<i>Carcinus maenas</i> (juv.)	..	..	..	..
Young plaice food...	ca. 453,000	54	135,400	166

NB: *Arenicola* only counted on 19 June, but the stock did not seem to have changed during the season.

4) Investigations on the wadden east of Skallingen in 1942.—On the wadden at Skallingen collections were made on August 13 and 14 1942 along the same sampling lines as were used by THAMDRUP (1935) (see the map in fig. 41). On line I 9 samples, and on line II 11 samples of $\frac{1}{100}$ m² were taken, and the results are shown in table 18. It turned out that conditions in 1942 were highly influenced by the previous three severe winters (SMIDT 1944 B), the older populations of several species (notably *Cardium edule*) having been greatly decimated, while on the other hand an abundant population of young was growing up, especially Lamelli-branches. Thus, at a single station (350 m from the edge of the wadden, on line I) the enormous number of ca. 72,000 0-group *Cardium* individuals per m² was observed. In 1943, however, this abundant brood had disappeared almost entirely, probably it had been consumed already in the autumn of 1942. It will appear from the tables how exceptionally large the quantity of young plaice food was precisely on account of the abundant *Cardium* 0-group. On line I there occurred between ca. 95 and ca. 848 g of young plaice food per m², and on line II between 21 and 243 g per m². The 848 g per m², found at the extreme outer station on line I, is the largest quantity of young plaice food ever registered at any station in the Waddensea.

the sand wadden north of Fanø.

10 October 1947									
ca. 300 m		420—430 m		0—25 m		ca. 170 m		ca. 440 m	
N	W	N	W	N	W	N	W	N	W
(30)	(0.1)	(20)	(<0.1)	340	1.4	(30)	(0.1)	(30)	(0.1)
(200)	(0.2)	10,000	5.4	..	..	(80)	(1.0)	500	5.9
..	..	(20)	(2.0)	..	..	..	..	..	..
..	..	..	..	(180)	(3.0)	(170)	(2.8)	..	..
(30)	(<0.1)	(120)	(0.1)	820	0.8	(50)	(0.1)	(230)	(0.2)
(30)	(0.1)	550	0.5	..	..	..	..	(30)	(0.2)
..	..	..	..	(80)	(<0.1)	(120)	(0.2)	..	..
..	..	..	..	2,200	6.2	..	..	..	..
7	0.4	4	0.2	18	1.1	28	1.7	4	0.2
..	..	..	..	..	..	..	..	1,100	1.1
90,000	137.6	175,000	209.7	(1,000)	(1.0)	77,000	77.0	106,000	476.0
15,000				..	..	..	..	41,000	
(100)	1.3	(100)	(0.1)	..	..	1,080	205.2	..	..
3,400	c. 3.0	1,500	1.0	(20)	(<0.1)	(120)	(1.0)	..	..
..	..	..	..	..	..	(70)	..	..	..
4,200	39.0	1,600	6.4	..	..	(130)	(0.3)	..	..
..	..	1,860	8.2	(40)	(0.1)	..	..	(70)	(0.2)
..	..	..	..	..	..	..	..	(70)	(0.1)
..	..	..	..	..	..	..	..	(70)	(0.1)
..	..	(30)	(0.1)	..	..	..	..	..	..
..	..	(30)	(0.3)	..	..	..	..	..	..
113,000	184	191,000	234	4,700	ca. 14	79,000	ca. 289	ca. 150,000	ca. 485

Table 14. Microfauna of the bottom on the sand wadden north of Fanø ca. 170 m from the low-water mark.

Date	1/7 1949		1/9 1949	
	N	W	N	W
Number and weight (g) per m ²				
<i>Harpacticoidea</i>	400,000	3.96	80,000	0.79
<i>Ostracoda</i>	15,000	1.79	32,000	0.38
<i>Nematodes</i>	434,000	2.17	182,000	0.91
<i>Scoloplos armiger</i> (0-group)	1,600	0.7	(<1,000)	(ca. 0.3)
<i>Nereis diversicolor</i> (0-group)	r	—	..	..
<i>Pygospio elegans</i> juv.	1,900	0.1	(<1,000)	(<0.1)
<i>Cardium edule</i> (0-group)	(900)	(0.2)	(<1,000)	(<0.1)
<i>Macoma baltica</i> (0-group)	(200)	(ca. 0.1)	..	..
<i>Hydrobia ulvae</i> (0-group)	4,000	0.4	..	..
<i>Bathyporeia</i> sp.	(300)	(0.5)	..	..
Total ...	858,000	9.9	312,000	2.4
Young-plaice food ...	424,000	7.7	113,000	1.5

Table 15. Macrofauna of the bottom on the sand wadden north of Fanø ca. 170 m from the low-water mark.

Date	¹ / ₇ 1949		¹ / ₉ 1949	
Number and weight (g) per m ²	N	W	N	W
<i>Phyllodoce maculata</i>	(10)	(0.2)	(30)	(0.4)
<i>Nereis diversicolor</i>	(10)	(3.5)	(10)	(5.5)
<i>Nephtys hombergi</i>	(20)	(3.0)	(10)	(2.5)
<i>Scoloplos armiger</i> { 0-group	(30)	(<0.1)	(80)	(0.2)
adults	600	20.5	440	21.0
<i>Pygospio elegans</i>	(40)	(0.1)	(80)	(0.2)
<i>Capitellidae</i>	(90)	(1.1)	(10)	(1.2)
<i>Arenicola marina</i> { hind parts	ca. 10	ca. 0.6	ca. 10	ca. 0.6
total		ca. 40.0		ca. 40.0
<i>Oligochaeta</i>	..	..	(10)	(<0.1)
<i>Cardium edule</i> (II-group)	450	704.0	480	812.0
<i>Macoma baltica</i> { I-group	(10)	(1.6)	(10)	(2.4)
older	(20)	(21.5)	(10)	(6.4)
<i>Bathyporeia pilosa</i>	(10)	(<0.1)	..	..
Total ...	ca. 1,300	ca. 796	ca. 1,180	ca. 892
Young-plaice food ...	ca. 680	ca. 30	ca. 690	ca. 34

NB: Numbers for *Arenicola* are those found in 1948; the stock does not seem to have changed since then.

Table 16. Microfauna of the bottom on the mud wadden off Nordby (Fanø).

Date	²⁸ / ₈ 1947		⁸ / ₁₀ 1947	
Number and weight (g) per m ²	N	W	N	W
<i>Harpacticoida</i>	15,000	0.15	50,300	0.50
<i>Ostracoda</i>	4,000	0.05	9,400	0.11
<i>Nematodes</i>	31,000	0.16	74,000	0.37
Total ...	50,000	0.36	134,000	1.0
Young-plaice food ...	19,000	0.2	60,000	0.6

5) *Mytilus* banks.—In several places in the outermost wadden areas, or in shallow-watered channels, densely populated *Mytilus* banks occur. Thus on the edge of the southern part of the wadden at Skallingen there is an extensive bank where THAMDRUP (1935) found numbers of individuals ranging between 2,000 and 12,000 per m² with a corresponding gross weight of ca. 9,500—ca. 32,000 g per m². On the opposite side of Ho Bay, in the outer zone of the large sand wadden off Sædding between Hjerting and Esbjerg, there are some extensive and very densely populated *Mytilus* banks, on which THAMDRUP (l. c.) found even up to 75 kg of *Mytilus* per m². These enormous quantities, however, are largely valueless as food for fish owing to the size of the Lamellibranchs; but it may be assumed that the newly settled brood of *Mytilus* may be utilised as food, similarly as some of the other epifaunal animals associated

Table 17. Macrofauna of the bottom on the mud wadden off Nordby (Fanø).

Date	²⁸ / ₈ 1947		⁸ / ₁₀ 1947	
Number and weight (g) per m ²	N	W	N	W
<i>Eteone longa</i>	(30)	(0.1)	(50)	(0.3)
<i>Nereis diversicolor</i> { 0-group	850	3.3	230	1.5
{ adults	..	..	(20)	(1.5)
<i>Pygospio elegans</i>	..	..	330	0.3
<i>Polydora ligni</i>	400	0.6	..	..
<i>Cirratulus cirratus</i>	(80)	(0.1)	(120)	(0.2)
<i>Capitellidae</i> sp.	800	4.6	830	14.6
<i>Oligochaeta</i>	ca. 300	ca. 0.5	230	0.3
<i>Hydrobia ulvae</i> (0-group)	550,000	271.2	..	..
<i>Cardium edule</i> (0-group)	5,200	130.0	..	..
<i>Macoma baltica</i> { 0- + I-group	(130)	3.6	(10)	(0.5)
{ II-group	r	—	..	..
<i>Scrobicularia plana</i> (0-group)	(100)	(13.0)	..	..
<i>Mya arenaria</i> (0-group)	11,600	42.9	(10)	(<0.1)
<i>Corophium volutator</i>	3,300	14.2	180	0.3
<i>Crangon vulgaris</i>	(30)	0.9	..	..
Total = young-plaice food...	573,000	485	2,000	20

with the banks, e. g. *Balanus* sp. and *Hydroidae*, may be consumed, as was shown by examination of the stomachs of *Limanda limanda*. In severe winters the mortality of the *Mytilus* populations is high, as was distinctly revealed by observations made at Skallingen in 1942 (SMIDT 1944 B) and off Sædding in 1947.

B. Channels.

1) The Microfauna.—Of the actual microfauna, the *Harpacticoidea*—as on the waddens—constitute a substantial part of the young plaice food, and, as shown in chapter V, they generally occur in smaller numbers in the channels than on the waddens. Newly settled brood of the macrofauna is likewise generally present in smaller quantities in the channels than on the waddens. Now, the areas in which sampling for the microfauna was carried out are shallow-watered, with depths of ca. 2–3 m, and with bottom qualities similar to those of the waddens, so in many instances a similar abundance of the microfauna to that on the waddens will be met with. No data are available from deeper water, but it is quite probable that the microfauna will be much poorer there.

For comparison between the microfauna of the channels and that of the waddens some figures will be given below:

In 1945, on sampling from ³⁰/₈ to ⁶/₉, the following quantities of young plaice food were found: on the sand wadden north of Fanø (4 samples of 5.7 cm², taken in the centre of the wadden) ca. 1 g per m², and at the channel stations along the stretch from southeast of Romø to southeast of Fanø (10 samples of 0.95 cm²) an average quantity of 0.6 g per m² was found.

In 1946 and 1947 micro-sampling was carried out at fishing stations in channels north and northeast of Fanø, east of Langli Sand, and in the interior of Ho Bay (table 19; the areas

Table 18. Macrofauna of the bottom

Distance from low-water mark	Line I, 14 August 1942					
	ca. 20 m		ca. 200 m		ca. 350 m	
Number and weight (g) per m ²	N	W	N	W	N	W
<i>Phyllodoctidae</i>	330	1.3	900	3.0	500	0.9
<i>Nereis diversicolor</i>	500	7.1	..	..	..	..
<i>Nephtys hombergi</i>	(30)	(0.4)	..	..	..	..
<i>Scoloplos armiger</i>	4,900	12.7	(150)	(3.0)	(150)	(1.0)
<i>Pygospio elegans</i>	300	0.3	500	0.2	2,300	1.0
<i>Cirratulus cirratus</i>	(200)	0.5	..	..	..	..
<i>Capitellidae</i>	1,800	7.7	1,500	12.8	600	6.9
<i>Arenicola marina</i> { hind parts	9	0.5	8	0.5	14	0.8
total		36.0		32.0		56.0
<i>Lanice conchilega</i> (juv.)	(70)	(0.1)	..	..	..	..
<i>Pectinaria koreni</i> (juv.)	(300)	(0.5)	..	..	..	..
<i>Oligochaeta</i> sp.	370	0.4	6,200	8.0	1,700	2.6
<i>Nemertini</i> sp.	..	..	(100)	(0.2)	..	..
<i>Hydrobia ulvae</i>	(130)	(0.3)	16,300	43.5	12,800	58.3
<i>Retusa obtusa</i>	..	..	..	..	(250)	2.6
<i>Cardium edule</i> { 0-group	36,000	771.0	55,400	269.0	71,800	156.0
adults	(70)	(740.0)	..	..	..	..
<i>Macoma baltica</i> { juv.	26,000	38.8	6,000	35.3	55,000	30.0
older	330	250.0	550	465.0	700	34.4
<i>Mya arenaria</i> (0-group)	8,800	6.4	1,300	1.1	300	0.3
<i>Corophium volutator</i>	(30)	(<0.1)	..	..	..	..
<i>Bathyporeia pilosa</i>	..	..	..	..	..	..
<i>Crangon vulgaris</i> (0-group)	..	..	..	..	..	..
<i>Carcinus maenas</i> (0-group)	..	..	(200)	1.7	(150)	(0.3)
Total...	107,400	1,874	89,500	875	96,700	351
Young-plaice food...	107,000	848	89,000	378	96,000	261

are designated Fanø, Langli, and Ho, respectively). In both years the samples were taken in June and October. In the table the figures for the sand wadden north of Fanø (150—170 m from the edge of the wadden) are given for comparison. The figures indicate the young-plaice food in grammes per m².

2) The Macrofauna.—In July—August 1941 a number of bottom samples of $\frac{1}{10}$ m² were taken in the southern part of the Waddensea. Ten of these, taken on the lines 5, 6, 7, and 13 (see the map in fig. 40, p. 121) at a depth of 3—16 m, gave the following average result:

	Number per m ²	Weight in g per m ²
Total bottom fauna	166	71
Food for young plaice	124	5

In the same area of the Waddensea (from the southernmost point of Rømø to some distance southeast of Fanø) fourteen bottom samples of $\frac{1}{10}$ m² were taken in shallow water from $\frac{30}{8}$ to $\frac{2}{9}$ 1945 (depth ca. $1\frac{1}{2}$ —3 m). At one of the samplings (southeast of Rømø) no less than ca. 320,000 individuals per m² were registered, almost all of them *Hydrobia ulvae*;

the wadden east of Skallingen.

Line II, 13 August 1942									
ca. 500 m		ca. 10 m		ca. 150 m		ca. 350 m		ca. 600 m	
N	W	N	W	N	W	N	W	N	W
(50)	(1.9)	(250)	(0.5)	(70)	(0.5)	..	..	..	..
(100)	(0.6)	(400)	14.3	(300)	(5.7)	530	4.3	(250)	4.5
..	..	..	..	..	..	..	..	..	..
..	..	1,720	11.5	..	..	..	..	..	..
600	0.4	..	..	5,600	1.4	(30)	(<0.1)	(200)	(0.2)
..	..	..	..	..	..	..	..	..	..
..	..	1,000	9.1	(30)	(<0.1)	..	..	..	..
r	—	34	2.2	5	0.3	r	—	..	..
..	..	306	..	20	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..
2,200	1.6	(250)	(0.3)	(200)	(0.6)	(200)	(0.2)	2,400	2.5
..	..	..	..	(100)	(1.0)	..	..	..	..
2,800	12.9	(400)	(1.6)	9,600	52.9	2,800	7.2	(200)	0.7
..	..	..	..	(170)	(2.5)	..	..	..	..
46,500	57.0	63,600	199.8	21,700	21.2	4,700	5.0	4,700	3.3
..	..	..	..	..	..	..	..	..	..
2,200	2.8	(450)	(2.3)	23,000	10.7	1,600	1.3	500	2.3
..	..	(ca. 10)	(ca. 6.0)	530	45.9	..	..	..	..
(100)	(0.1)	..	..	..	..	..	..	..	..
9,200	16.8	(50)	0.1	3,900	7.0	1,300	2.4	17,400	21.1
..	..	..	..	(200)	0.6	(30)	(0.1)	(50)	(0.1)
..	..	..	..	(130)	(1.4)	..	..	(50)	(0.5)
1,000	0.8	(50)	1.0	(200)	(1.1)	(30)	(0.1)	(50)	(0.2)
65,000	95	ca. 68,000	555	45,500	173	11,000	21	25,800	35
65,000	95	ca. 68,000	243	45,000	107	11,000	21	25,800	35

the weight was 459 g per m², of which *Hydrobia ulvae* constituted 448 g. But apart from this rich sample, the other thirteen samples were poor in content, their average values being as follows:

	Number per m ²	Weight in g per m ²
Total fauna.....	394	ca. 75
Food for young plaice	378	26

In the northern part of the Waddensea 23 bottom samples of $\frac{1}{10}$ m² distributed over six different stations (see the map in fig. 41 p. 122) were taken from August 3 to 10, 1942, at depths between ca. 2 m and ca. 8 m. The results of these samplings are shown in table 20, from which it appears that the quantity of young-plaice food varied between 1—2 and ca. 17 g per m².

Altogether these figures show distinctly that generally the quantities of young-plaice food per m² are much smaller in the channels than on the waddens, and the total weight also, and notably the numbers of individuals, are much lower in the channels. Further, it will be seen that the deeper parts of the channels are poorer in young-plaice food than the more shallow-watered areas, as will appear from a comparison between the samples from the southern

Table 19. Young-plaice food of the microfauna.

	Sand wadden	Channels			
	N. of Fano	Fano	Langli	Ho	
1946, 20—22 June					
Actual microfauna	5.5	3.2	2.1	1.9	
Brood of macrofauna	4.7	2.3	1.8	0.5	
Total...	ca. 10	5—6	ca. 4	2—3	
1946, 15—19 Oct.					
Actual microfauna	0.1	0.1	6.1	5.9	
Brood of macrofauna	0.1	..	..	..	
Total...	ca. 0.2	ca. 0.1	ca. 6	ca. 6	
1947, 14—16 June					
Actual microfauna	6.6	0.1	6.1	inner	outer
Brood of macrofauna	..	..	..	0.9	6.9
Total...	ca. 7	ca. 0.1	ca. 6	ca. 1	ca. 7
1947, 10—15 Oct.					
Actual microfauna	0.5	0.3	0.4	very little	
Brood of macrofauna	ca. 2	..	..	..	
Total...	2—3	0.3	0.4	very little	

NB: In June 1947 two stations were taken in Ho Bay (an outer and an inner).

Waddensea from 1941 and 1945 and a comparison of the various stations in the northern Waddensea in 1942. It should be added that the cause of the scarcity of animals at station D (table 20) is its position at the mouth of the river Varde Aa, where large quantities of fresh water flow out.

C. Summary and discussion.

It was shown in the preceding pages that it is on the waddens that the great production of young-plaice food takes place, while compared with them the channels as a whole are poor in food elements. The causes of the paucity of the food in channels as compared with the waddens, can only be conjectured; but an essential cause is probably to be found in the fact that the channels harbour a great many consumers which may soon eat up the tiny brood. These consumers include not only the fish, but also large numbers of *Carcinus maenas*, *Eupagurus bernhardus*, *Crangon vulgaris*, and *Asterias rubens*, which together must be an effective factor in keeping down the population of sessile bottom animals. Another factor is the effect of the substratum mentioned in chapter VI, p. 92—93, which must especially be able to make itself felt in the wadden areas in furthering the settling of the pelagic larvae.

In chapter IX it was shown that the 0-group plaice immigrating at the beginning of the summer (in June and the beginning of July) feed on the microfauna, and it is noteworthy that precisely at this time of the year by far the greatest quantities of microfauna are present on the waddens. Of the actual microfauna, the *Harpacticoidea* constitute by far the most import-

Table 20. Macrofauna of the bottom in the channels in the northern part of the Danish Waddensea 3—10 August 1942. (Valuation with the van Veen bottom-sampler).

Locality	Hamborg Dybet		Esbjerg Havneleeb		Ho Bay							
	St. H		St. E		St. A		St. B		St. C		St. D	
Depth	ca. 3 m		ca. 8 m		ca. 6 m		3—4 m		ca. 2 m		ca. 2 m	
Number and weight (g) pr. m ²	N	W	N	W	N	W	N	W	N	W	N	W
<i>Sagartiogeton undatus</i>	..	..	..	..	10—20	..	..	..	..	..	..	..
<i>Harmothoe imbricata</i>	..	..	..	..	<10	ca. 0.4	..	..	..	..	..	..
<i>Phyllodoce maculata</i>	} <10		..	..	c. 100	ca. 0.3	} c. 100	c. 0.5	..	..	..	..
<i>Eteone longa</i>			..	..	..	..			..	..	..	..
<i>Nereis diversicolor</i> (juv. + old.)	<10		<10	c. 1	ca. 30	ca. 1.2	ca. 30	c. 0.1	..	..	} ca. 30	c. 1.3
<i>Nereis virens</i>	..		..	..	..	..	..	..	..	..		
<i>Nephtys hombergi</i> (juv. + old.)	<10		<10	c. 2.5	ca. 30	ca. 2.1	..	..	..	..	..	..
<i>Goniada norvegica</i>	..		<10	<0.1	..	..	..	..	..	..	..	..
<i>Scoloplos armiger</i> (juv. + old.)	120		200	5.6	600	2.2	780	5.3	ca. 50	<0.1	..	..
<i>Pygospio elegans</i>	..	15	ca. 30	<0.1	..	..	c. 250	ca. 0.1	c. 300	<0.1	..	..
<i>Polydora ligni</i>	..		..	..	..	..	ca. 30	ca. 0.1	..	..	..	..
<i>Cirratulus cirratus</i>	..		..	..	ca. 50	ca. 0.1	ca. 30	<0.1	..	..	..	..
<i>Ophelia limacina</i>	..		ca. 20	c. 0.2	..	..	..	..	..	..	..	..
<i>Capitellidae</i> sp.	<10		..	..	..	..	<10	<0.1	..	..	..	..
<i>Pectinaria koreni</i>	..		<10	c. 1.3	ca. 20	ca. 0.5	ca. 10	<0.1	..	..	..	..
<i>Lanice conchilega</i> (juv.)	..		ca. 80	..	..	..	..	..	..	..	..	..
<i>Oligochaeta</i> sp.	<10		..	..	380	0.1	1,820	1.3	ca. 50	<0.1	..	..
<i>Nemertini</i> sp.	..	..	..	..	..	..	ca. 80	ca. 0.8	..	..	..	..
<i>Retusa</i> sp.	..	..	..	..	..	..	20—30	ca. 0.3	..	..	..	..
<i>Cardium edule</i> { 0-gr.	..	..	..	..	..	..	..	..	600	1.0	..	..
{ older	<10	..	..	..	..	..	..	..	..	..	..	..
<i>Macoma baltica</i> { 0-gr.	..	..	..	..	<10	ca. 0.4	..	..	..	..	..	..
{ older	..	..	+	..	<10	..	ca. 30	..	ca. 20	..	..	..
<i>Mya arenaria</i> 0-gr.	..	..	..	..	..	..	400	0.8	..	..	ca. 10	ca. 0.2
<i>Mytilus edulis</i>	..	..	..	..	ca. 10	..	..	..	..	..	..	..
<i>Corophium volutator</i>	..	..	..	..	..	..	7,400	7.1	4,600	7.7	..	..
<i>Pycnogonid</i> sp.	..	..	..	..	<10	<0.1	..	..	..	..	..	..
<i>Gammarus</i> sp.	..	..	..	..	..	..	ca. 80	ca. 0.5	..	..	..	..
<i>Carcinus maenas</i> juv.	..	..	..	..	<10	..	20—30	ca. 0.2	..	..	..	..
<i>Eupagurus bernhardus</i>	..	..	..	..	ca. 10	..	..	..	..	..	..	..
<i>Asterias rubens</i>	..	..	<10	..	ca. 10	..	<10	..	..	..	..	..
Total ...	ca. 150	..	ca. 350	..	c. 1,200	..	11,100	..	5,600	..	ca. 40	..
Young-plaice food ...	ca. 150	ca. 15	ca. 340	ca. 10	c. 1,200	7	11,100	17	5,600	9	ca. 40	1—2

ant food element, and, as was shown in chapter V, this animal group attains a maximum in June. Also that part of the microfauna which is constituted by the brood of the macrofauna, is most numerous at the beginning of the season; this applies especially to *Hydrobia ulvae* and the Lamellibranchs (notably *Cardium edule*). Instructive in regard to the quantitative occurrence of the microfauna are the values for the wadden north of Fanø (150—170 m from the edge of the wadden) for 1946:

	²² / ₆ 1946	¹⁵⁻¹⁶ / ₁₀ 1946
Actual microfauna.....	ca. 5 g per m ²	ca. 0.1 g per m ²
Brood of macrofauna.....	ca. 5 g per m ²	ca. 0.1 g per m ²
Total young-plaice food of microfauna	ca. 10 g per m ²	ca. 0.2 g per m ²

For the macrofauna, also, the values from the same locality and the same dates are highly instructive; thus on ²²⁻²⁶/₆ 1946 ca. 8 g of young plaice food per m² was registered, while on ¹⁵⁻¹⁶/₁₀ 1946 this quantity had risen to ca. 119 g per m². This increase is largely due to the production of a numerous population of 0-group *Hydrobia ulvae*. On the whole it is the year's production of bottom animal brood which constitutes the main part of the immense quantities of young-plaice food on the waddens, as will appear from the tables for the wadden north of Fano in 1946 and 1947, the soft wadden at Nordby in 1947, and the wadden at Skallingen in 1942. Hence years in which the production of brood fails will exhibit only small quantities of food, as was apparently the case in 1943, 1948, and 1949. As an example to show the colossal importance which this production of brood may have, it may be mentioned that on the wadden at Skallingen, at a single station (near low-water mark on line I) no less than ca. 848 g of young plaice food per m² was found; of this quantity the 0-group of *Cardium edule* constituted by far the greater part.

Precisely because it is the year's production of bottom animal brood which constitutes the chief part of the young-plaice food, this will be subject to great quantitative variations both in the course of the year and from one year to another. Years with a rich brood, as for instance 1942 and 1947, will mean abundant young-plaice food, while years with poor broods will have the opposite effect. On account of these great fluctuations it will be difficult to say anything of general validity about the quantity of fish food present on the waddens, but according to the experience gained in the northern part of the Waddensea we may perhaps regard the 84 g per m² which was found as an average for the quantity of young-plaice food present on the waddens throughout the whole southern part of the Danish Waddensea in the summer of 1941, as representing approximately the lower limit of the quantity that usually occurs; probably ca. 100 g per m² will be nearer the normal quantity of young-plaice food.

Finally it should be mentioned that the damage done by severe winters to the bottom animal population of the waddens does not reduce the possibilities of the succeeding summer for a good production of fish food, for these communities are not closed, but thanks to the lively currents will always have a possibility of obtaining a supply of pelagic brood from other, undamaged, areas. In the two summers of 1942 and 1947, both following upon severe ice winters, even exceptionally large quantities of newly produced brood occurred. Possibly the conditions for a good settling of brood are even better in such years in which the population of older bottom animals has been decimated than in years with a dense population of older age-groups, a phenomenon which seems to apply especially to *Cardium edule*, as was mentioned by THAMDRUP (1935, p. 71) and SMIDT (1944 B, p. 18), and as would seem to be confirmed by the production of a numerous 0-group of *Cardium* in the summer of 1947 after a severe winter.

Whether a numerous 0-group is capable of surviving during the next season, and the succeeding seasons also, depends not only on the severity of the winter cold, but to a great extent also on the consumption during the first summer. Thus it turned out that the numerous 0-group of *Cardium* from 1942 had totally disappeared already the next summer. Another striking example of the reduction of the population by the consumers is afforded by 1947,

when the numerous 0-groups of *Cardium edule* and, especially, of *Mya arenaria* were so much reduced that the *Mya* population disappeared entirely (see table 7, p. 117). A particularly heavy reduction took place of *Hydrobia*, *Cardium*, and *Mya* on the soft wadden at Nordby that year, the young-plaice food in the period $^{28}/_8$ to $^8/_{10}$ being reduced from ca. 485 g per m² to only 20 g per m². The colossal reduction of the *Hydrobia* 0-group that takes place every year is likewise an expression of the activity of the consumers. As to the Lamellibranchs, it can be said that if they survive the first year or the first two years, they will have attained such a size that the majority of them will escape the persecution of enemies. Thus it turned out that the *Cardium* population of the year-class 1947 was not subject to any demonstrable reduction in the course of the season of 1949.

In the next chapter some comparisons will be made between the quantitative conditions of the bottom fauna on the waddens and those of other sea areas, where this fauna is of importance as food for the fish stock.

XII. The Production on the Waddens compared with the Production in other Areas.

In the preceding chapter the production of food for young flatfish in the Waddensea was dealt with. It will be of interest, now, to make a comparison between this area and other waters where the bottom fauna likewise serves as food for a population of flatfish.

A. The microfauna.

In chapter V the actual microfauna on the waddens was compared quantitatively with the corresponding fauna in other seas. It appeared from the comparison that the microfauna on the waddens (both in the Danish Waddensea and in the Bristol Channel (REES 1940)) is richer than in deeper water.

B. The macrofauna.

In table 21 (p. 138) values from various marine shallow-watered areas have been compiled, showing the total number of individuals, the total weights, and the weights of first-class fish-food. All the values apply to a bottom area of 1 m².

The concept first-class fish-food was erected by BLEGVAD (1925 and 1930) on the basis of examinations of the stomach contents of various fish feeding on bottom animals, chiefly flatfish. According to BLEGVAD this fish food includes worms, smaller Crustaceans, and small thin-shelled Lamellibranchs and *Gastropoda*. Second-class fish-food comprises such animals as may be consumed by the fish in the absence of other food. This applies for instance to *Aphrodite aculeata*, thick-shelled small and medium-sized Lamellibranchs (e. g. *Corbula gibba*) and *Gastropoda*, and a number of *Echinoderma* (Ophiurans, small *Echinocardium*). The third group, that entirely without value as food, comprises the big thick-shelled Lamellibranchs and *Gastropoda*, the big *Echinoderma*, and the largest *Crustacea*. It will be seen that the group first-class fish-food is very nearly the same as is termed young-plaice food in the present paper,

Table 21.

Region	Community	Locality etc.	Number of indi- viduals	Total weight	1. class plaice food		Source
			(average)	(average)	average	max.	
Danish Waddensea	<i>Macoma</i>	Waddens { southern area, July-Aug. 1941 at Skallingen Aug. 1942....	31,000	174 g	84 g	200 g	
			63,600	497 g	249 g	..	
Ringkøbing Fjord	<i>Macoma</i>	Tidal areas at { July-Aug. 1937..... the Tipper { July 1938..... June 1939.....	3,176	26.7 g	26.7 g	..	Spärck (unpubl.)
			3,190	42.4 g	42.4 g	..	
			2,427	45.0 g	45.0 g	..	
Dybso Fjord	<i>Macoma</i>	Depth ca. 0.1-1.9 m	844	55.2 g	55.2 g	..	Larsen (1936)
Cuxhaven	<i>Macoma</i>	America Harbour, depth ca. 7 m.....	75,300	270 g	73 g	..	Hagmeier (1925)
	<i>Macoma</i>	Poor localities.....	59	6.9 g	5.4 g	..	
		Rich -	358	30.8 g	18.2 g	..	
Heligoland Bay	<i>Syndosmya</i>		700	105.4 g	76.0 g	..	Hagmeier (1925)
	<i>Venus</i>	Northeastern area	113	28.2 g	12.4 g	..	
		Southwestern -	273	25.1 g	4.8 g	..	
	<i>Amphiura</i>	Mixed with elements of:					
		<i>Venus</i> -community	406	98.1 g	14.6 g	..	
		<i>Syndosmya</i> -community	1,770	232.8 g	33.9 g	..	
Limfjord	<i>Syndosmya</i>	Thisted Bredning (18 years invest.)...	..	..	44.7 g	136.6 g	Blegvad (1928)
		Lovns - (13 - -)...	..	..	48.9 g	279.6 g	
		Sallingsund (12 - -)...	..	..	62.2 g	336.8 g	
Kattegat	<i>Venus</i>	Several years' investigations in various localities.....	808	46.3 g	23.9 g	97.0 g	Blegvad (1930)
			368	26.8 g	10.7 g	15.8 g	
			344	71.0 g	18.2 g	82.7 g	
			121	100.6 g	8.8 g	9.1 g	
	<i>Amphiura</i>	Several years' investigations in various localities.....	657	216.6 g	21.6 g	30.6 g	
			309	219.5 g	10.1 g	13.8 g	
			277	138.6 g	22.0 g	30.5 g	
	<i>Haploops</i>	Two years' investigations	1,458	54.9 g	34.4 g	54.9 g	

so the author thought it permissible to compare these two groups directly, as is done in the table, in which the term first-class fish-food has reference to both. It should be pointed out, however, that the young-plaice food as here defined only include the youngest Lamellibranchs (for *Cardium edule* and *Mya arenaria* only the 0-group, for *Macoma baltica* possibly the I-group also), so the concept young-plaice food is a little more limited than the concept first-class fish-

food. THAMDRUP (1936) gives some very high figures for the quantity of first-class fish-food (plaice food) on the wadden at Skallingen in the years 1932, 1933, and 1934. These figures seem, however, to have been calculated somewhat too high (at any rate they are a good deal higher than the quantity of young-plaice food), so in the table I have only used my own values from the Waddensea.

The columns of the table first indicate the geographical areas, all of which are Danish or situated near Denmark: the Kattegat, the Limfjord, and Dybsø Fjord (at the Great Belt) are inner Danish waters, while the other areas belong to the west coast of Jutland, the German North Sea coast, and the southern part of the North Sea. Then follows the community examined (designated in accordance with the terminology of C. G. J. PETERSEN). In some cases a more limited locality within the geographic area or community is indicated, or different periods of investigation are given. Further, the table gives the density of individuals, the total weights, the quantity of the first-class fish-food, and finally, the source whence the information was derived.

The figures of the table are average figures for several stations within the particular area investigated, and in a number of cases for several years. In some cases the maximum values are given; for the southern part of the Waddensea in 1941 they have reference to the wadden area in which the largest quantity was collected, while the maximum values for the Limfjord and Kattegat have reference to the time when the largest quantities were found.

As far as the Waddensea is concerned, the average values for the southern area for 1941 are regarded as representing the normal (though they are probably somewhat below the normal), while the mean values for the wadden at Skallingen for 1942 must be regarded as indicating approximately the richest young-plaice food that may occur on the waddens at all. It should be added that the areas in the Limfjord included in the table are the richest within this water.

Comparing, now, the mean values for the Waddensea with those for other areas, it will be obvious how immensely richly populated the waddens are. The average numbers of individuals on the waddens far exceed those found in other places, which is due to the fact that the fauna is characterised by comparatively many small individuals (either of small species such as *Pygospio elegans*, *Hydrobia ulvae*, and *Corophium volutator*, or of brood of bigger species). Only the samples from Cuxhaven exhibit an abundance of individuals exceeding that of the waddens, but we are here concerned with a locality which belongs to the German Waddensea, even though it is no wadden locality (as on the waddens, it is chiefly *Hydrobia ulvae* and young *Mya arenaria* and *Cardium edule* which constitute the largest numbers). Considering the average total weights, we shall find that they are high for the waddens as compared with most other places, and it should even be pointed out that both the two seasons, 1941 and 1942, followed upon very severe winters, which had greatly reduced the older populations of bottom animals, so the total weights found must be regarded as lower than the normal. Finally it will be seen that the average quantities of first-class fish-food range higher on the waddens than in any other place, but that, as regards the maximum occurrences of fish food, the weights found in the Limfjord far exceed those found on the waddens. But altogether it can be said that the waddens, compared with other sea areas, are exceptionally rich in fish food.

It is noteworthy that the locality in Ringkøbing Fjord, in which the natural conditions are much like those of the Waddensea (a wadden locality with a *Macoma* community), likewise exhibits an abundance of individuals and large quantities of fish-food, though to a lesser extent than the Waddensea. The rich locality at Cuxhaven should probably be regarded as a some-

what special locality. Of the other areas, those in which *Syndosmya* communities occur (Limfjord) seem to be rich, and the *Haploops* community in the Kattegat is likewise especially rich in individuals and presents a comparatively large quantity of fish food.

Particularly large quantities of bottom animals have been found in patches in several places. Thus, as mentioned in the preceding chapter, in 1942 the weight of the total quantity at a single station on the wadden at Skallingen was found to be 1874 g per m², and the young plaice food 848 g per m². But even larger quantities—likewise in patches—have been found in other places also. Thus HAGMEIER (1930, p. 139) states that in a limited area off the East Frisian coast a total of 5,258 g per m² was found, and out of this 4,280 g first-class fish-food per m². By far the greater part was constituted by *Spisula subtruncata*.

It is characteristic of the areas richest in first-class fish-food that the quantities of this fish food are subject to great fluctuations from year to year. This applies, besides to the Waddensea, i. a. also to the Limfjord (BOYSEN JENSEN 1919, BLEGVAD 1925 and 1928) and the Dogger Bank area in the North Sea (DAVIS 1923). In all these areas the annual production is, as a rule, high, practically all the first-class fish-food present being produced afresh every year. On the waddens this food is constituted almost entirely by the brood of various bottom animal species (chiefly *Cardium edule*, *Hydrobia ulvae*, and various *Polychaeta*), and in the other areas it is especially certain biologically annual Lamellibranchs that constitute the main quantity (in the Limfjord primarily *Syndosmya alba* and *nitida* and *Cultellus pellucida*, and on the Dogger Bank mainly *Spisula subtruncata*). Precisely because this first-class fish-food is produced afresh every year, the great fluctuations from year to year will be understandable, the quantity depending on whether the particular year was a good or a poor breeding year. For the Waddensea such good and poor breeding years have been demonstrated above. It is, however, impossible to give a complete estimate of the annual production of this brood, since production and consumption continually take place during the season, and we have no measure for the consumption. An estimation of the amount of the consumption on the waddens might be obtained if it would be possible to protect certain areas against the consumers (notably fish and birds) without, in doing so, preventing the settling of brood. By comparing the quantity of fish food at the beginning and the end of the season in these areas and in unprotected areas the production as well as the consumption might be determined.

XIII. Summary and Future Work.

In the present paper the author has attempted to give an all-round description of the fauna of the Waddensea and its ecology, the main object having been a study of the animal production within the area. From the literature it appears that the Frisian Waddensea is the chief nursery ground of the youngest year-groups of the plaice population of the North Sea (the 0-, the II-, and possibly the III-group), and the author has endeavoured to ascertain the quantity of food available for these young plaice, and the production and consumption of this quantity of food.

Chapter II contains a description of the technique employed in collecting the plankton samples, the samples of the micro- and macrofauna of the bottom, and the quantitative treatment of these samples.

The topography and hydrography of the Waddensea are described in chapter III, chiefly on the basis of the literature and on information supplied by co-workers at the Skalling Laboratory. A distinction is made between channels, which are constantly filled with water, and the so-called waddens, which are dry during the diurnal low-tide. The waddens are divided into waddens with a firm sandy bottom, those with a soft muddy bottom, and those with a mixed bottom; the waddens with a soft bottom occur only in sheltered places with considerable movements of the water. The hydrography is primarily characterised by the tide, which recedes twice in twenty-four hours, leaving dry ca. 60 per cent. of the area of the Danish Waddensea, and gives rise to very strong tidal currents. Moreover the Waddensea exhibits much greater variations of temperature and salinity than the North Sea outside.

In chapter IV the biological importance of the Waddensea for fishery is treated on the basis of the literature and the working journals of the Marine-Biological Laboratory; further, a characterisation of the fish fauna with a list of the species of fish present is given. Of a certain importance are a local fishery and digging of *Arenicola marina* for bait, but it is undoubtedly as nursery ground for the plaice population of the North Sea that the Waddensea has its chief significance. From spawning grounds in the southern part of the North Sea the young plaice migrate to the shallow water along the coasts of Holland, Germany, and Denmark, where the growth takes place during the summer half-year. In the winter half-year they migrate to deeper water, returning next spring to the shallow water, where plaice up to three years old are commonly met with feeding during the summer half-year.

As it turned out that the microfauna of the bottom is of great significance in regard to the animal production, the author subjected this faunal element to special study (Chapter V). The concept of microfauna, which is briefly discussed, is defined as that part of the bottom fauna which escapes capture if the usual sampling technique is employed, so a special micro-sampling was carried out. The microfauna is divided here into the actual microfauna, including the animals which preserve their microfaunal character throughout their whole life (notably *Nematodes*, *Harpacticoidea*, *Ostracoda*, and *Foraminifera*), and the brood of the macrofauna. The quantitative collections here and in the Bristol Channel (REES 1940) show that the true microfauna is particularly numerous in tidal areas, compared with other sea areas. The animal group of the true microfauna that is of greatest importance for the 0-group plaice, viz. the *Harpacticoidea*, attains its frequency maxima in June and the beginning of July, precisely at the time when the 0-group plaice immigrate into the Waddensea.

Chapter VI first contains a characterisation of the bottom macrofauna of the Waddensea based mainly on earlier investigations carried out in the Danish and the German Waddensea. On the waddens the infauna (the *Macoma baltica* community) constitutes the principal faunal element, but in addition there occur a sessile and a vagile epifauna. In the channels the infauna consists in part of a *Macoma baltica* community mixed more or less with constituents of the adjoining communities in the North Sea (*Syndosmya alba* and *Amphiura filiformis* communities), but the epifauna, more especially the vagile epifauna, is the principal faunal element in the channels, where *Crangon vulgaris* is particularly numerous and constitutes an important food element for fish. Chapter VI further contains a list of the macrofaunal bottom species found in the Danish Waddensea and an account is given of the biotopes in which they live; finally the occurrence of the most important species in relation to the ecological factors is discussed.

The life histories of the macrofaunal bottom species of greatest significance viewed from the angle of animal production are treated in chapter VII, their reproduction, growth, and mortality having been studied. The greater number of these species have a long pelagic larval

development, while two species (*Scoloplos armiger* and *Corophium volutator*) have a non-pelagic, and two species (*Arenicola marina* and *Hydrobia ulvae*) have a much shortened pelagic development. The very abundant settling of pelagic brood observed on the waddens must be assumed to be due to a particularly strong effect of the substratum when the areas are flooded by the tide and large water masses come into intimate contact with the bottom. This view is supported by some substratum experiments with larvae of *Pygospio elegans* and *Polydora* as well as by numerous examples of the effects of the substratum on various animal groups, i. a. Lamellibranchs, recorded in the literature. Great fluctuations in the quantities of settled young from one year to another were observed, which suggest the occurrence of good and poor years of breeding. In several cases it turned out that while the adult bottom animals exhibit frequency maxima in certain zones of the waddens, the young are most numerous in other zones. Thus the young *Arenicola marina* are most abundant on the higher-lying portions of the sand waddens, while the adults are most frequent in the lower-lying areas. Conversely, the adult *Hydrobia ulvae* and *Nereis diversicolor* are, as a rule, concentrated near the high-water mark, while the young are most numerous on the outer and middle parts of the waddens. Measurements of the growth were carried out on several species; for species growing for more than one season a lively growth was observed during the summer half-year and a stagnation during the winter half-year. The quantitative investigations of the individual species revealed a heavy depletion of the year's brood in the course of the summer half-year due to consumption. An extraordinarily great mortality among the populations on the waddens is caused by severe ice winters.

In chapter VIII the occurrence of the various zooplanktonic organisms during the year as well as their varying occurrence due to the tide are discussed. A number of organisms were much more numerous, and some were only observed, in samples taken at high-water, so they must be assumed to have been carried in with the tidal current from the outer part of the Waddensea or from the North Sea. As examples of such organisms the larvae of the bottom animals *Magelona papillicornis*, *Lanice conchilega*, *Coecum glabrum*, *Bela turricola*, *Venus gallina*, and several Echinoderm larvae may be mentioned. A number of these will settle in the Waddensea, where they will perish, while others are carried out with the falling tide. Other larvae that are produced in abundance in the inner parts of the Waddensea were most numerous, or at any rate numerous, in the low-water samples, as was the case with *Pygospio elegans* (larval type III), *Polydora*, and *Littorina littorea*. As the larvae of the bottom animals living on the waddens are also produced outside these areas, the wadden fauna may always be recruited afresh even if severe winters play great havoc among the populations of adult animals on the waddens. The occurrence of the larvae in the course of the year exhibits a minimum in January—February. In the spring the larvae of the species inhabiting the tidal areas begin to appear, the adults of these species being stimulated to spawn owing to the early heating of the shallow water by the sun. An exception is formed by *Arenicola*, which is so deeply buried in the bottom that it will not be influenced by the heating by the sun in the spring. It is not till later in the year that the larvae of most of the species living in deeper water will appear.

In chapter IX the food of the bottom fauna is treated on the basis of the available literature, and it is regarded as highly probable that the chief source of food for the invertebrate fauna of the waddens is the rich flora of bottom diatoms.

Of the consumers of the bottom fauna, which are treated in chapter X, young plaice, *Gobius minutus*, *Crangon vulgaris*, and migratory birds must be regarded as the most important, as far as the waddens proper are concerned. Comprehensive examinations of the stomach contents of

plaice have shown that for the newly immigrated individuals of the 0-group the main food consists of small crustaceans (on the sand waddens especially *Harpacticoidea*, in Ho Bay primarily the brood of *Corophium volutator*). Later in the summer the food of the 0-group, like that of the older year-groups, is more varied, consisting chiefly of the year's production of bottom animal brood. In the channels *Crangon vulgaris* and *Mysis flexuosa* are especially pursued by the consumers. On examination of the stomach contents of plaice it turned out that if abundant and varied food was present, one food element might be especially preferred. Thus in the summer of 1947, when rich 0-groups of both *Cardium edule* and *Mya arenaria* were present, the latter was practically exterminated, while a considerable stock of *Cardium* survived, this year-group being abundantly represented on the waddens in the succeeding years.

In chapter XI the results of valuations on the waddens and in channels are treated, and it appears that as regards both the total quantities of animals present and the food of the young plaice in general the waddens are much richer than the channels. It is shown that the microfauna (the true microfauna as well as the young individuals of the macrofauna) is most abundant in June and the beginning of July, precisely at that time of the year when the 0-group plaice have such a small size that this faunal element constitutes their main food. As far as the macrofauna is concerned, the quantities of young-plaice food vary greatly both in the course of the year and from one year to another.

Comparisons with other sea areas, as made in chapter XII, show that such a great production of young-plaice food as on the waddens hardly takes place in any other area; consequently they must be regarded as being of very great importance for the economy of the North Sea.

There are a number of problems concerning details which have not been solved in the present investigation, but which it would be desirable to include in future investigations. The following may be mentioned:

1) A more detailed examination of the biology of the true microfauna as far as reproduction and food is concerned.

2) Certain special studies of the macrofauna of the bottom, notably the following points: a) The systematic interrelationship of *Polydora ciliata* and *P. ligni*, it being assumed that we are here concerned with only one species with a certain range of variation; b) the reproduction of *Heteromastus filiformis*, in order to ascertain whether the lecithotrophic larvae described belong to this species; and c) the migrations of *Arenicola marina*.

3) A detailed study of other sources of nutrition for the bottom fauna than the bottom diatoms and the plankton diatoms; attention should especially be directed towards the bacterial flora.

4) An investigation of the interrelation of production and consumption. This might perhaps be carried out by closing off minor areas of a wadden for the consumers without thereby preventing the settling of young. By comparing the quantity of the fauna per areal unit within and outside the closed-off areas at the beginning and the end of the season (e. g. in April and October), it might be possible to estimate the amount of both the production and the consumption.

Dansk Resumé.

Der er i dette arbejde søgt givet en alsidig beskrivelse af Vadehavets fauna og dens økologi, hvorved hovedsynspunktet har været studiet af områdets produktionsbiologi. — Af litteraturen fremgår, at det frisiske Vadehav er det vigtigste opvækstområde for de yngste årgange af Nordsøens rødspættebestand (0-⁴⁰ II- evt. III-gruppen), og i det foreliggende arbejde er der da lagt vægt på at undersøge fødemængden for disse unge rødspætter og produktionen og konsumet af denne fødemængde.

I kapitel II er givet en beskrivelse af teknikken ved indsamlingen af planktonprøver, mikrobundprøver og makrobundprøver samt den kvantitative behandling af disse prøver.

Vadehavets topografi og hydrografi er beskrevet i kapitel III, hovedsagelig på grundlag af litteratur og oplysninger fra medarbejdere ved Skallingelaboratoriet. Der skelnes mellem render, der til stadighed er vandfyldte, og vader, der tørlægges ved daglig lavvande. Vaderne deles i de med ¹⁾ fast sandbund, ²⁾ blød mudderbund og ³⁾ blandet bund. Af disse forekommer blødbundsvader kun på læbeskyttede steder med ringe vandbevægelser. De hydrografiske forhold er først og fremmest karakteriserede ved tidevandet, der 2 gange i døgnet tørlægges ca. 60 % af det danske Vadehavs areal, og som bevirker meget kraftige tidevandsstrømme. Desuden frembyder Vadehavet langt større svingninger i temperatur og saltholdighed end Nordsøen udenfor.

I kapitel IV er der på grundlag af litteratur og Marinbiologisk Laboratoriums arbejdsjournaler gjort rede for Vadehavets fiskeribiologiske betydning, og desuden gives der en karakteristik af fiskefaunaen med en fortegnelse af de forekommende fiskearter. — Af en vis økonomisk betydning er et lokalt fiskeri samt gravning af sandorme til agn, men det er utvivlsomt som opvækstområde for Nordsøens rødspættebestand, at Vadehavet har sin største betydning. Fra gydeområder i den sydlige Nordso vandrer de unge rødspætter ind på det lave vand langs Hollands, Tysklands og Danmarks kyster, hvor opvæksten sker i sommerhalvåret. I vinterhalvåret vandrer de ud på dybere vand for næste forår atter at søge tilbage til det lave vand, hvor indtil tre år gamle fouragerende rødspætter træffes almindeligt i sommerhalvåret.

Da det viste sig, at bundens mikrofauna spiller en betydelig produktionsbiologisk rolle, gjorde forfatteren dette faunaelement til genstand for særlige studier (kapitel V). — Begrebet mikrofauna, der gøres til genstand for en kort diskussion, defineres her som den del af bundfaunaen, der unddrager sig den sædvanlige boniteringsteknik, hvorfor en særlig mikrobonitering foretoges. Mikrofaunaen inddeles her i den ægte mikrofauna, der hele livet tilhører denne del af faunaen (særlig *Nematodes*, *Harpacticoidea*, *Ostracoda* og *Foraminifera*), og de yngste bundstadier af makrofaunaen. De kvantitative indsamlinger her og i Bristol Channel (REES 1940) viser, at den ægte mikrofauna er særlig talrigt tilstede på tidevandsarealer i sammenligning med andre havområder. Den dyregruppe af den ægte mikrofauna, der har størst betydning for 0-gruppe rødspætte, nemlig *Harpacticoidea*, har hyppighedsmaximum i juni og i begyndelsen af juli, netop på den tid, da 0-gruppe rødspætte vandrer ind i Vadehavet.

I kapitel VI gives først en karakteristik af Vadehavets makrobundfauna, hovedsagelig baseret på tidligere undersøgelser i det danske og det tyske Vadehav. På vaderne er ifaunaen (*Macoma baltica* samfund) det vigtigste faunaelement, men dertil kommer en fastsiddende og en bevægelig påfauna. I renderne består ifaunaen delvist af et *Macoma baltica* samfund mer eller mindre iblandet bestanddele af de tilgrænsende samfund i Nordsøen (*Syndosmya alba* og *Amphiura filiformis* samfund), men iøvrigt er påfaunaen, og ganske særlig den bevægelige, det vigtigste fauna-

element i renderne, hvor navnlig hesterejer er meget talrige og udgør et vigtigt fødeemne for fiskene. — Videre gives der i dette kapitel en fortegnelse over de i det danske Vadehav fundne arter af makrobundfaunaen med en redegørelse for på hvilke biotoper de lever, og endelig diskuteres de vigtigste arters forekomst i relation til økologiske faktorer.

Livshistorierne for de produktionsbiologisk vigtigste arter af makrobundfaunaen behandles i kapitel VII, idet deres forplantning, opvækst og dødelighed er blevet studeret. De fleste af disse arter har lang pelagisk larveudvikling, mens 2 arter (ormen *Scoloplos armiger* og slikkrebsen) har upelagisk og 2 arter (sandormen og sneglen *Hydrobia ulvae*) har en meget stærkt afkortet pelagisk udvikling. Den meget talrige bundfældning af pelagisk yngel, der er observeret på vaderne, må antages at skyldes en særlig stærk substratvirkning, når tidevandet overskyller disse arealer, hvorved store vandmasser kommer i intim kontakt med bunden. Denne anskuelse understøttes foruden af nogle substratforsøg med larver af ormene *Pygospio* og *Polydora* tillige af de talrige eksempler fra litteraturen på substratvirkning hos forskellige dyregrupper bl. a. også muslinger. — Der har vist sig store svingninger i mængden af bundfældet yngel fra år til år, hvilket tyder på forekomsten af gode og dårlige yngelår. — I flere tilfælde viser det sig, at medens de voksne bunddyr har hyppighedsmaxima i visse zoner af vaderne, er ynglen talrigst i andre zoner. Således forekommer de unge sandorme talrigst på de højereliggende dele af sandvaderne, mens de voksne er hyppigst i de lavere liggende områder. Omvendt findes de voksne *Hydrobia ulvae* og *Nereis diversicolor* som regel koncentreret nær højvandslinien, mens ynglen findes talrigst på den ydre og mellemste del af vaderne. — Vækstmålinger er udført på flere arter og viser for de arter, der vokser i mere end een sæson, en livlig vækst i sommerhalvåret og en stagnation i vinterhalvåret. — De kvantitative undersøgelser af de enkelte arter har vist et meget stort svind blandt årets yngel i løbet af sommerhalvåret, hvilket skyldes konsumet. En ekstraordinær stor dødelighed blandt bestandene forårsages af strenge isvintre.

I kapitel VIII behandles de forskellige zooplanktonorganismers — især bunddyrlarvernes — forekomst året igennem og deres vekslende forekomst med tidevandet. En del organismer forekommer langt talrigere og nogle udelukkende i prøver taget ved højvande, hvorfor de må betragtes som værende ført ind med tidevandsstrømmen fra den ydre del af Vadehavet eller fra Nordsøen. Som eksempler herpå kan blandt bunddyrlarverne nævnes *Magelona papillicornis*, *Lanice conchilega*, *Coeum glabrum*, *Bela turricola*, *Venus gallina* og flere pighude-larver. En del af disse vil bundfælde inde i Vadehavet, hvor de da går til grunde, mens andre atter føres ud med ebbestrømmen. Andre larver, der produceres i store mængder inde i det indre af Vadehavet, findes talrigst eller i hvert fald talrigt i lavvandsprøverne, således som tilfældet er med larver af ormene *Pygospio* og *Polydora* og sneglen *Littorina littorea*. Da larverne til de på vaderne levende bunddyr også produceres uden for disse områder vil vade faunaen altid kunne nyrekrutteres, selv om strenge vintre har hærget bestandene af voksne dyr på vaderne. — Larvernes optræden i årets løb viser et minimum i månederne januar—februar. I forårs-månderne begynder larver af tidevandsområdernes arter at optræde, idet de voksne dyr af disse arter stimuleres til gydning på grund af solens tidlige opvarmning af det lave vand. Undtagen herfra er sandormen, der sidder så dybt nedgravet, at den unddrager sig solens opvarmning om foråret. Først senere på året optræder de på dybere vand levende arters larver.

I kapitel IX gennemgås på grundlag af foreliggende litteratur bundfaunaens ernæring, og det betragtes som overvejende sandsynligt, at den vigtigste grundnæringskilde for vadernes bundfauna er den rige flora af bunddiatomeer.

Af bundfaunaens konsumenter, der behandles i kapitel X, må opvoksende rødspætter,

kutlinger, hesterejer og fugleflokke regnes for de vigtigste, når talen er om selve vaderne. Omfattende maveundersøgelser af rødspætter har vist, at for de nyindvandrede af 0-gruppen er små krebsdyr (på sandvaderne især *Harpacticoida*, i Ho Bugt særlig yngel af slikkrebs) hovedføden. Senere på sommeren tager 0-gruppen ligesom de ældre årgange en mere varieret føde, som overvejende udgøres af årets produktion af bunddyryngel. I renderne efterstræbes især hesterejer og *Mysis flexuosa* af konsumenterne. Ved undersøgelserne af rødspættemaverne viste det sig, at når der var rigelig og varieret føde til stede, kunne eet fødeemne være særlig foretrukket. Som følge heraf sås det i sommeren 1947, da der var rige 0-grupper af både hjertemusling og sandmusling, at sidstnævnte blev praktisk talt udryddet, mens en betydelig bestand af hjertemusling overlevede, så årgangen genfandtes på vaderne følgende år i anseelige antal.

I kapitel XI behandles resultaterne af boniteringer på vaderne og i render, og heraf fremgår, at vaderne både med hensyn til totale kvanta og med hensyn til føde for opvoksende rødspætter i almindelighed er langt rigere end renderne. Det vises, at mikrofaunaen (både den ægte og ynglen af makrofaunaen) er til stede i størst mængde i juni og begyndelsen af juli, netop på den tid af året, hvor 0-gruppe rødspætterne har en sådan størrelse, at dette faunaelement er deres hovedføde. — Med hensyn til makrofaunaen viser der sig store variationer i mængden af opvækstføde både i årets løb og fra år til år.

Sammenligninger med andre havområder, som er foretaget i kapitel XII, viser, at der næppe noget sted foregår en så stor produktion af opvækstføde for rødspætter som på vaderne, hvorfor de må betragtes som havende en meget stor betydning for Nordsøens økonomi.

En del detaillerspørgsmål, som ikke er løst ved den foreliggende undersøgelse, vil det være ønskeligt at få taget op ved fremtidige undersøgelser. Her skal fremdrages følgende:

1) En nøjere undersøgelse af den ægte mikrofaunas biologi med hensyn til forplantning og ernæring.

2) Visse specialundersøgelser af makrobundfaunaen, hvoraf følgende særlig skal nævnes: a) *Polydora ciliata*'s og *P. ligni*'s indbyrdes systematiske forhold, idet det formodes, at der her kun er tale om een art med en vis variationsbredde, — b) forplantningen hos *Heteromastus filiformis* for at konstatere om den beskrevne lecithotrofe larve tilhører denne art, — c) sandormenes vandringer.

3) En nærmere undersøgelse af andre næringskilder for bundfaunaen end bunddiatomeerne og planktondiatomeerne, idet opmærksomheden særlig bør rettes mod bakteriefloraen.

4) En undersøgelse af forholdet mellem produktion og konsum, som tænkes udført ved, at mindre arealer af en vade afspærres fra konsumenterne uden at bundfældning af yngel derved hindres. Når da faunaens kvantitet pr. arealenhed inden for og uden for de afspærrede arealer sammenlignes ved begyndelsen og slutningen af sæsonen (f. eks. i april og i oktober), skulle det være muligt at bedømme størrelsen af såvel produktion som konsum.

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